Systems Ecology and Limits to Growth: History, Models, and Present Status

History, Models and Present Status

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Abstract

Systems ecology, including systems science more generally within or associated with the discipline of ecology, started with a great deal of enthusiasm and four main areas of development a little more than half a century ago, propelled by new hardware, software, and conceptual developments. Issues pertaining to the survival and sustainability of modern industrial civilization, and indeed humans themselves, have been intertwined with systems ecology more or less since the start of each. Obvious examples include the Limits to Growth models and many subsequent analyses of sustainability (or lack thereof). Systems ecology today is far more diffuse and fragmented than it was a half century ago, although it lives on in the general use of modeling and the many concerns about the planet's future. These include: climate issues, ecological footprint analysis, energy analysis (including EROI, or energy return on investment), emergy analysis, Hubbert energy analyses, ecological economics, and biophysical economics. Since most of these efforts include at least some means of dealing with complex data sets, and indeed complexity itself, then one can say that systems ecology is alive and well and continuing to deal with the issues that were part of their original focus. But general public and political interest, never strong, is even less so at this time even though the original concerns initiated some 50 years ago are far more clearly defined and operational today. Probably the main reason is that the price of gasoline at the pump is not perceived as being especially high (unless you are poor, or in France or much of Africa, in which case it is devastatingly so). The perceived success of fracking has led to the perspective in the minds of most Americans that technology will continue to resolve issues of scarcity, as indeed it appears (quite arguably) to have been the case so far. While most of the world may not be concerned, the issues raised by the founders of Systems Science continue unabated and to the degree they have been mitigated it is primarily through increasing energy use, most of which is carbon-based. If we are to decrease our use of carbon-based energy, the transition will be extremely difficult and will require the use of much systems science. Even with the greatest efforts, it is not clear that it is possible.

Keywords

Ecology · Economics · Energy · IASSA · IBP · Limits to growth · Models · Odum · Systems ecology · Systems

Introduction

Civilizations have been growing and collapsing since at least the birth of cities some 8000–10,000 years ago, and probably long before that. Indeed Mesopotamia, the region of the origin of both agriculture and cities, is strewn with the massive ruins of the first cities, including ancient Ur, the origin of our word urban. Surely ancient scholars were aware of this pattern of growth and collapse and must have thought long and hard about the causes, although they were perhaps as likely to attribute the demise of cities to the will of the gods as to our present favorite determinants, which include the erosion of soils, climate changes, diseases, the shifting of rivers, resource depletion, corruption of leadership, military excursions, and so on. Prophets, including many priests, the oracle at Delphi or Cassandra, the princess of ancient Troy, often foretold the demise of their cities (in her case Troy, which indeed was destroyed). More modern assessments, if not exactly prophecy, perhaps can be said to begin with the work of historians such as Edward Gibbon's six volume work "*The History of the Decline and Fall of the Roman Empire*" (Gibbon, 1776–1789), Ostwald Spengler's work "*The Decline of the West*" (Spengler 1922), and blossomed with the work of archeologist/anthropologist/historian Joseph Tainter (1988). His rather incredible synthesis "The collapse of complex societies" gave a general mechanism for collapse: the necessary development of energy-requiring complexity as political systems and central cities expanded, increasing their need for imported food and other resources which had to come from further and further away. Eventually they could not afford to maintain that complexity. All historians deal with the complexity of factors that generate, sustain, and cause the demise of cultures, and thus are systems scientists, with or without computer models. The growth and demise of cultures continues to be a fertile area for the application of concepts and tools generated within or parallel with Systems Ecology. I get in my email inbox various assessments of the probable collapse (or occasionally the unlikelihood of collapse) of modern societies or economies nearly daily.

Systems science, that is, the formal quantitative study of complex entities, evolved in the first half of the twentieth century, once the tools allowing such analyses were developed. Two main tools were needed: (1) the development of "systems thinking," the simultaneous integration of many components (vs., e.g., the two component approach in Cartesian mathematics – when in fact in many real systems there may not be a single causative agent but many) and (2) a means of solving many mathematical equations simultaneously or nearly so. Such approaches and devices were being constructed to do things such as predict tides, since at least the early nineteenth century by, for example, Charles Babbage (1791–1871) and Ada Lovelace (1815–1852). They were greatly accelerated during World War II, with its specific origins often attributed to the English defenses for the battle of Britain. This required the integration of the new technology of radar, the position of oncoming German airplanes and both the aiming of the English antiaircraft guns and positioning of the fighter planes so that, ideally, they could attack the German planes optimally, such as by "coming out of the sun". Under the remarkable and prescient direction of General Hugh Dowding, the system was in place with hundreds of miles of buried and hardened telephone lines connecting the various pieces by the time the battle of Britain began in August 1940 (Korda 2010). Perhaps as important to both the war effort and to systems science was the derivation of electronic devices to break the German enigma code, with which the third Reich communicated with its armies and submarines. This was done at Bletchley Park under the direction of intellectual direction of Allen Turing. Since at that time conventional analytical mathematics essentially could not solve more than two equations simultaneously, a means was found to solve large systems of equations quickly with electronics and triode vacuum tubes. Almost certainly England, and the Allies more generally, could not have held off the German invasion of England without systems science and these (and other) remarkable minds and electronic devices. England eventually showed its appreciation for these great patriots who saved England by relieving Dowding of command and putting Turing in jail for being a homosexual. Nevertheless it is remarkable that the government of England recognized the threat and put the resources into dealing with and resolving it. Given the various environmental and resource threats facing our contemporary civilization, one wonders about our own government that not only does not deal with, but often denies the various threats, such as depletion, epidemics and climate change.

Following the war these new devices and their improvements had many applications, mostly in engineering, including flight and battle simulators, and various governmental and commercial applications. To give a sense of what these new electronic means for solving mathematical equations meant, one can refer to the thoughts of mathematician John Kemeny, who was involved with the development of the Atomic bomb. In the summer of 1944 one half of all mathematicians in the United States convened in Los Alamos, New Mexico, to compute secretly the fluid dynamics equations for the exploding atomic bomb. It took them all summer and many hundreds of Monroe calculators to conclude that the force of the explosion would push the atoms of U_{235} apart rapidly enough so that the chain reaction would not destroy the world – a distinct possibility according to some physicists. Later, Kemeny (1926–1992), then President of Dartmouth, provided every freshman an Apple II, a first-generation personal computer. He said that one good undergraduate with an Apple II could solve those fluid dynamics equations in an afternoon. The key was using incremental (finite difference) equations recursively. These were much easier to solve, and generally more powerful, than trying to solve the same equations with pure analytical or closed form mathematics. Obviously, this enormous increase in computational power meant many things.

Ecology, Systems, and Modeling

A number of coalescing patterns encouraged the development of a systems approach in ecology and its application to the larger issues of mankind. I was very much involved in this development, first as a graduate student near its inception and then as a “medium-level” participant and contributor. My orientation was to approach and attempt to understand these developments as one trained in the natural sciences, with very little input from the social sciences. Thus I am well positioned to write this review, although I wish to make it clear that it is almost entirely from the perspective of a natural scientist, even when I make excursions into what others might consider the proper role of the social scientists. Others in this volume will cover that as they see fit.

Perhaps most important in the initiation of systems ecology was the publication of Eugene Odum's Fundamentals of Ecology textbook in 1953. (He had proposed to teach a course by that name to his faculty of biology at the University of Georgia and had been laughed out of the room with: "There are no principles in ecology". He started writing that textbook that afternoon, which in time made him by far the best known and probably wealthiest member of that faculty). Odum argued that ecology should most properly be the study of ecosystems, as opposed to the study of individual species, a perspective that had dominated ecology teaching before that time. Also important was the simultaneous tremendous development of nuclear technology, both for war and peace, and the realization by many that we knew very little about the fate and transport of radionuclides in natural environments. Large and well-funded laboratories were initiated at Savanna River, South Carolina, Oak Ridge, Tennessee, and Hanford, Washington to study these issues. Other, less extensive programs were initiated in, e.g., Puerto Rico and at Brookhaven National Laboratory. All of these programs both promoted an ecosystems perspective and provided a lot of funding for ecologists, a tale beautifully told by Joel Hagen (Hagen 1992).

The Formal Development of Systems Ecology

First, what is a system? According to Donella Meadows, it is a "Purposeful set of components, interactions and rules for interacting" (Meadows 2008). According to Montague (2014) "the origin of the term "systems ecology" and the breadth of this then new field are found in E. P. Odum's "The New Ecology" (Odum 1964). Gene Odum saw computers and the mathematical systems approach as powerful means to advance theory of ecosystem self-organization and establish principles of ecosystem management." The concept of systems ecology was enormously developed by Gene's younger brother Howard Thomas (H.T.), who started as a biologist at the University of North Carolina where his father, also named Howard, was a very influential systems-oriented and quantitative sociologist. H.T. served as a lieutenant in the Army air force in the Caribbean during WWII where he was undoubtedly influenced by the large-scale weather systems of the tropics, such as Hadley cell circulation. When he got out of the Air force, he did a PhD with G. Evelyn Hutchinson at Yale, the outstanding mentor for ecologists at that time. Odum did his PhD dissertation on the global biogeochemistry of strontium, which was soon to be of interest as a radioactive by-product of nuclear explosions. Armed with these global-level studies H.T. became enamored with the patterns and complexity of energy flow in ecosystems, and he, occasionally with his brother, undertook a series of very innovative procedures to measure the rate at which energy flowed through the main components of various ecosystems (e.g., Odum and Odum 1955). The most important was a study of Silver Springs, Florida, a large "boil" of very clear fresh water fed by underground limestone river systems (Odum 1957).

Odum thought long and hard about how to summarize and visualize the energy flow through Silver Springs (Fig. 1). He then developed a series of graphic modules

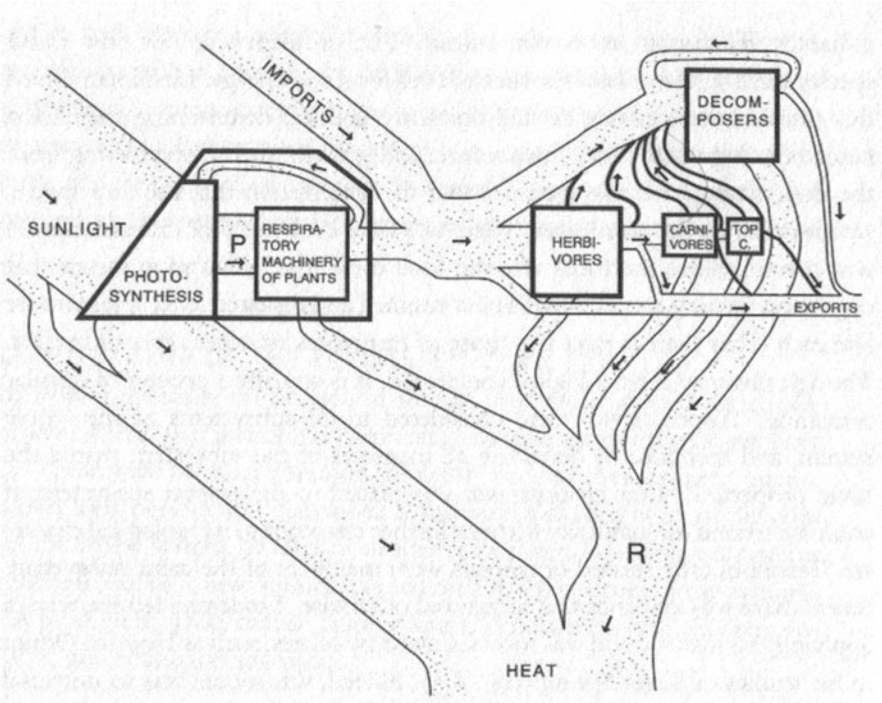


Fig. 1 Energy diagram: energy and matter flows through an ecosystem, adapted from the Silver Springs model. P is gross photosynthesis and R is respiration. Squares represent biotic pools and arrows are fluxes of energy and nutrients through and from the system

adapted from electrical circuitry to represent these mostly biotic processes (Fig. 2). In a way this made a great deal of sense as both electrical and ecological systems are the story of how electrons get a kick in the pants by a generator or battery in the one case, or by photons captured in photosynthesis, and then is passed through a series of steps where the energy is transferred and utilized to do work until the electron is back at the ground state, or terminal electron acceptor, be it the other pole of the battery or oxygen in the environment. As part of this Odum developed a series of generalized symbols representing energy sources (most usually the sun) outside the system, state variables (biological entities), flows between state variables, storages, control modules (called "work gates"), and so on (Fig. 3). Once you became familiar with the approach it represented a very logical way for organizing the basic information of an ecosystem (or any system). Perhaps the most important conceptual innovation was to think of nature not as a series of individuals, or species, but rather as groupings (initially trophic or food groupings: primary producers, consumers, first carnivores, decomposers and so on). In this way the enormous diversity of the different ecosystems around the world could be understood as similar conceptual models. Later Odum used these symbols to represent other, often physical, systems such as rivers, hurricanes, stars, and also human-dominated systems such as agriculture,

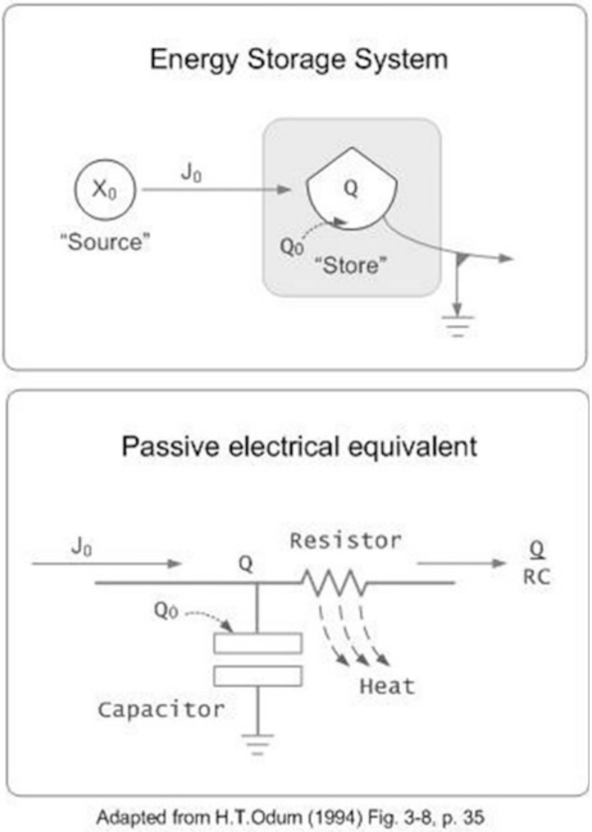


Fig. 2 Howard Odum's "electric analogy" between electronic circuit modules and energy symbols

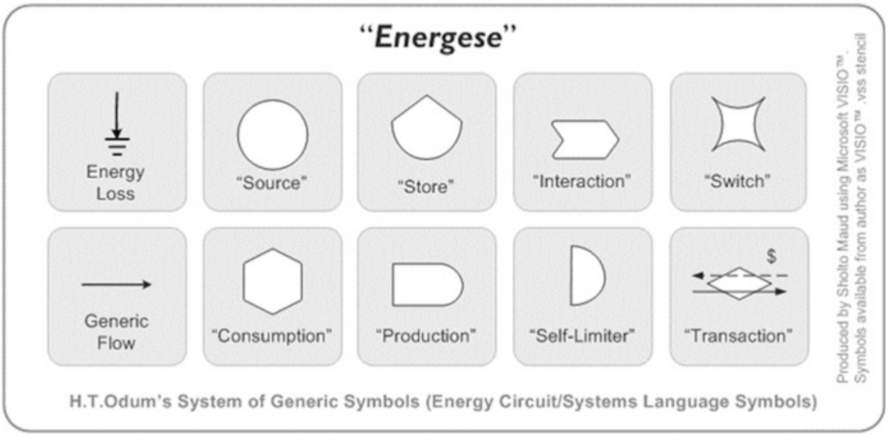


Fig. 3 H.T. Odum's generic system of energy symbols

cities and national economies, showing how all were beholden to the same energy principles. Sholto Maud (1996) has written a fascinating paper showing how Howard Odum realized Liebnitz's dream of a generalized language for much of the world's systems.

The development of computer models was not lost on ecologists. The first computer models in ecology were very different from our perception of computer models now. Howard Odum, influenced by his boyhood enthusiasm for the book "The Boy Electrician," viewed wires as analogous to trophic (food) pathways, capacitators as analogous to storages of energy within a trophic level (i.e., biomass), resistors as energy flowing into respiration or predators and triodes or transistors as "work gates" where one energy flow influenced larger energy flows (such as energy invested by a predator into catching a prey). He built the first models of energy flows in ecosystems (and perhaps the first models of any type in ecology) using radio parts, and generated a list of new ecosystem principles derived from his early experiments and measurements (Odum 1960; Table 1). Subsequently commercial analog computers became available, and trophic pathways could be set up by plugging in connecting wires from one trophic component to another. My introduction to models was initially a room full of green metal boxes connected by wires, with a huge wheel with 3 by 5 cards cut out to follow the daily tracings of solar input to the Luquillo Forest of Puerto Rico. I initially learned computer programming by plugging in

Table 1 Hints about ecosystems derived from the analogue circuit. The construction and manipulation of the analogue is a powerful stimulant to the imagination concerning the behavior of ecosystems. The following are some suggestions from the analogue for experimental testing in the real ecosystems. The tests employed were made with the circuit in steady states resembling natural systems such as Silver Springs. (From Odum 1960)

1. Competition exists when two circuits are in parallel
2. Consumer animals compete with plant respiratory systems
3. When unusual biomass and ecoforce distributions (potentials) are postulated, circuits reverse direction with food passing in unusual directions. For example, with large rates of import of organic matter, energy flows into the plants heterotrophically increasing plant respiration over its photosynthesis
4. As sources of power, the primary producers and the import system compete
5. If shunts exist with bacteria in important roles, a steep pyramid of metabolism develops
6. If consumer respiration is increased, gross photosynthesis is also increased due to the lowered resistance
7. Doubling the power supply doubles the metabolism at all levels
8. Cutting off export increases metabolism of consumers
9. Cutting off top carnivores does very little to the remainder of the energy flows
10. Increasing import increases respiratory metabolism and diminishes gross photosynthesis
11. Cutting out herbivores reduces photosynthesis and increases bacterial and plant respiration
12. Higher trophic levels compete in part with the trophic level which it consumes
13. A change in plant respiration has a major compensatory effect on the consumers
14. A decrease in respiration increases the voltage (biomass concentration) upstream
15. A short circuit is comparable to a forest fire

wires and setting potentiometers (variable resistors) on such a device. In a sense, we were doing the same thing as the early English modelers.

By the mid-1960s analog devices had given way to digital computers, and computers were coming into general usage at national laboratories, universities and many businesses (Shea 2017). There were four major efforts in ecological modeling underway. The first was the International Biological Program (IBP), a large and ambitious program at (principally) Oak Ridge National Laboratory, Colorado State and Oregon State Universities focusing on obtaining and modeling basic ecosystem-level information on five basic ecosystems types, including grasslands and Eastern deciduous forests (Coleman 2010). The second was the efforts of several ecologists at the University of Georgia, including Richard Wiegert, Eugene Odum, and especially Bernard Patten. The third was a broad push to understand and simulate natural ecosystems and eventually "man and nature" by Howard Odum at the Universities of North Carolina and Florida. Finally a diverse effort was underway by independent researchers focusing principally on resource management such as tree-insect pest interactions, including efforts by Buzz Holling, Charles Warren (e.g., Warren et al. 1979) and Kenneth Watt.

Most of these efforts, including, in time, Odum's, used digital computers, originally mostly gigantic IBM mainframe devices. Some examples of these early efforts include: soil decomposition (e.g., Olson 1963), movement of radioactively labeled elements, ecotoxicology and, later, impact of power plants on fish (Hall 1977).

Howard Odum was probably the first ecologist to explicitly include humans in his models, not as much from a sense of human impact on nature but more to include humans as important components of ecosystems. This is perhaps best seen from his 1973 book "*Environment, Power and Society*". He developed a series of increasingly complex and sophisticated approaches to understanding and quantifying ecosystems, first of nature alone and then of "man and nature", as diagrams in that book. In all of his work he emphasized the role of energy in driving ecosystem processes, and he pioneered a series of methods for measuring energy stocks and flows. Odum believed very much in a general systems approach: and modeled cities, hurricanes, and stars using the same general approach, circuit diagrams, and equations that he used for ecosystems. In a sense his monumental "*Ecological and General Systems*" (the second edition of his *Systems Ecology*) is as general a systems approach to all the world's knowledge as exists. "If the bewildering complexity of human knowledge in the 20th century is to be retained and well used, unifying concepts are needed to consolidate the understanding of systems of many kinds and to simplify the teaching of general principles." Odum attracted very many students and scientists from all around the world who found that his approach helped a great deal with complex problems they were working on. There is a "family tree" of his students and associates as of about 1994 in the introduction to Hall's "Maximum Power" (1995b).

Meanwhile Bernie Patten was generating a series of usually more theoretical approaches to understanding ecosystems (e.g., Patten 1959; Patten and Odum 1981; Patten and Auble 1981). He also was organizing a series of meetings at the University of Georgia on Systems Ecology which resulted in a series of four large and often intimidating books on the logic, mathematics, and applications of various perspectives on Systems Ecology (Patten 1973–1975). They provided a unifying perspective for what Systems Ecology was becoming, in the view of many, from a descriptive and perhaps philosophical approach to ecology to a more quantitative, mathematical and, in the view of many, rigorous approach to the complexity of nature. Perhaps the most characteristic words for me, then and now, were complexity and intimidating mathematics. Meanwhile Kenneth Watt published several books providing a general approach to systems ecology with an emphasis on management, and George Van Dyne summarizing the IBP ecosystem measuring and modeling studies (Watt 1966; Van Dyne 1969; Coleman et al. 2004).

Somewhat later Hall and Day (1977) provided a less intimidating and perhaps more uniform introduction based on the systems approach of Howard Odum. When I recently reread the first introductory chapter, I felt that that it still provides a good summary of what we are still trying to do, with the exception of the very changed environment of writing computer code. The book also provided many examples of how these models could be applied to such varied fields such as fighting wild fires, managing nutrients in estuaries, and assessing environmental impacts of power plants (e.g., Hall 1977). Some of these models, or their descendants, were used for decades and are even still used.

Personal Note

I was a PhD student of Howard Odum from 1967 to 1970 at the University of North Carolina, along with a large number of rather remarkable graduate students. It was a fantastic experience, like nothing I have seen in academia before or since (Hall 1995b). Most of us were focused on ecology with a small e, that is, on trying to understand how nature operated. This was before the first Earth Day, and usually when you were talking up some young lady at a party you had to explain what the word "ecology" meant. For us grad students it was extremely exciting to be around Odum as we were exposed to a much larger view of ecology and its importance through his systems approach, his willingness to tackle any problem (especially if it was "big"), and his remarkable intelligence and enthusiasm. I have never seen such intelligence in all the years since, both in terms of innovation and in understanding how things work. In addition, it was great fun (Hall 1995b)! We grad students would often remark that, when standing next to Odum as he interacted with one and then the next person in the "Odum train" of people following him from place to place (he was professor in three departments) that it was like standing next to a big electricity dynamo. Your hair would stand on end from the induced flow of electrons as the massive intellectual transformations took place as he gave each person in turn requesting his attention unique and very useful interpretations of the problem he or she was working on. While his very complex diagrams and (sometimes) mathematics could be confusing, intimidating, and even off-putting, I, and essentially all of us "Odumites", agreed with Tom Butler who said "once you strip Odum of his special language it's just common sense". But it was a new, synthetic, and all-encompassing kind of common sense. Even with all of this I found Odum to be a real southern gentleman. He could be tough (and even scary) on his students and on his critics, but he always listened to what one had to say and treated people who had less power with gentleness and respect. Howard Odum personified one of my favorite descriptions: "The mark of a gentleman is that he does not mistreat the help."

His main idea was that by understanding the general nature of ecosystems and of systems in general one would not have to start from scratch for each new situation. Even if the species names might be quite different, the general nature and operation of all of them followed a series of general rules or at least regularities, all regulated by energy costs and gains and the Darwinian selection for maximum power. Perhaps the main feature of his systems approach to ecology was looking at nature "in ecos," that is, as it is, in its actuality and complexity and in its biotic and abiotic entirety. This contrasts sharply with most conventional science, which tends to focus on isolating a section of a system and undertaking careful test and controlled studies of a very specific issue.

At the time I was with Odum (1967–1970), he was shifting, with encouragement from his wife Virginia, from undertaking studies of natural ecosystems (streams, estuaries, coral reefs, tropical forests) to human-dominated systems (cities, sewage lagoons, and industrial society generally), probably catalyzed by watching the great petroleum towers near Houston increasingly towering over the estuaries in which he was measuring biological energy flow with "diurnal" (technically diel) analyses of oxygen (Swaney and Hall 2004). I think for him the new petroleum–dominated systems were just another Ecosystem, although one with more intensive infrastructure and energy flow. Oyster reefs and cities were similar for him, both just centers of consumption of energy, each requiring large areas of production elsewhere whose products had to be carried in by external "energy subsidies," tides in the case of one and oil in the case of the other.

While we were in Graduate school, there was an explosion of information and predictions about the environmental problems and the degrading state of the Earth, including Paul Ehrlich's book "*The Population Bomb*" (Ehrlich 1960) and the original renditions of "*The Limits to Growth*" (Forrester 1971; Meadows et al. 1972) as well as general environmental concerns expressed by George Woodwell, Kenneth Watt, Garrett Harden, and others which could not help but get the attention of graduate students in ecology. Collectively, these made a very large change in the perspective of many people and led to the initiation of Earth Day, the formation of some important environmental groups such as The Environmental Defense Fund and the US Environmental Protection agency, expanding the horizon of jobs for us. There were more than a few signs of ecology having a much larger and more important role in the general ordering of human affairs (e.g., Taylor 1988; Hagen 1992). I will return to a more detailed discussion of the limits to growth later.

There was a general sense that ecologists understood these issues better than most others, and that there was some kind of special understanding of things that came from ecological knowledge. Concepts such as "limits" and "carrying capacity" were transferred from ecology to predicting the human condition. One had the sense that ecology was going to take its rightful place among the very most important disciplines, and that systems ecology was going to be leading the effort (Hall et al.

2017a). Along with the hippies of the time, ecology students aspired to "change the world." This time period also saw the initiation and development of the United States Environmental Protection Agency and considerable environmental legislation suggesting that the world was indeed changing, or at least might change, for the better. Many of us viewed all this very optimistically. For myself and for most of Odum's other graduate students, we were sure we were learning the keys to the future (e.g., Mitsch 1994; Ewel 2003).

Although it cannot be said that ecologists had any particular input to the development of the Limits to Growth models it is probable that the general sense of the limits to the Earth for supplying the needs and desires of humanity, the growing increase in the human population and its consequences, and the general increase in environmental destruction all led to the intellectual milieu within which the LTG models evolved.

From a student's perspective, systems thinking (in general) and Systems Ecology (in particular) offered insight into the structures and interconnections (e.g., stocks and flows, usually in terms of energy) of natural processes, leading to an understanding of phenomena as they occur in reality, that is as complex and interconnecting systems, and through such concepts as *emergent properties*, that is properties of the system that were not deliberately put into the models but emerged from their operation. The holistic and systems approach to address problems or questions, whether in an ecological context or otherwise (e.g., energy or economics) provides a comprehensible framework to break down complexity, while forcing connections to be acknowledged and understood. Ultimately, we have found that a systems method of thought serves as a very useful way to approach, organize, and in some cases solve many, many problems (e.g., Hall and Day 1977).

Relation of Models to Systems Science

From the beginning systems ecology and modeling were practically synonymous; once you were introduced to the concepts of systems ecology it was expected that you would go on to the next stage: defining, conceptualizing, building and running some kind of model. But, in systems ecology (and in general) what is a model? Hall and Day (1977) give three definitions: (1) a meaningful simplification of a real system (2) a device for predicting the behavior of a complex entity whose behavior is not known from the operation of its parts, whose behavior is known, and, the one I prefer, (3) a formalization of our knowledge about a system. Within this context, they viewed models as not necessarily computer entities but as: (1) conceptual models (2) diagrammatic models, (3) mathematical or quantitative models, and (4) computer models. The process of generating mathematical or (especially) computer models was generally that of building *algorithms*, that is a logical sequence of mathematical statements. To do this, once the conceptual and mathematical models were derived, was to derive *functional relations* between parameters and then to simulate (or model) their collective behavior. Usually "iterative loops" (DO loops or FOR loops in many computer languages) were used to solve and update the equations over time and/or space. Of course, there were many devils in the details! But the real strength of the models, in my mind at least, were in sensitivity analysis (where one could examine the response of the model to parameters or structures that were not known with precision (i.e., *sensitivity analysis*), and in the examination of the behavior of the model components relative to that of the real system in question (i.e., *validation*). By undertaking sensitivity analysis and validation, a great deal can be learned about the real system, including what you do not know.

Most of the models that have been developed in ecology are for quite specific uses, usually a particular problem for a particular ecosystem. This probably reflected funding sources, which were usually interested in particular problems, not general models. Examples found in Hall and Day (1977) include carbon flow through Barataria Bay, Louisiana, food chains in Apalachicola Bay, Florida and Narragansett Bay, Rhode Island, growth of forests in New Hampshire, spread of fire in Montana, and many more. Many of the basic models could be exported (I used the Rhode Island model, slightly modified, for plankton in the Pacific Ocean and Flathead Lake Montana). Probably many of these old models would be quite applicable to new ideas today.

There is a general sort of tradeoff about systems models in whether we are, or should be, generating specific models for specific problems or whether it would be more efficient to build general models that all or many modelers would then apply to their particular problems, rather like engineers or economists. While it is true that theoretical modelers tend to use the logistic population model over and over that seems not the same, because, as developed below, such models have rarely been effectively validated. A partial exception may be the Leslie Matrix, a population model whose strength is that it is almost true by definition. All it requires is good empirical data on birth rates and survivability by size. Ahh, but here's the rub – the data are very difficult to get! But it is possible to get good data, if care and resources are applied (e.g., Goodman 1982, 1987). Curiously, since different ecosystems tend to have somewhat the same trophic structure there does not seem to be a generally accepted trophic model from those days where one would just plug in the specific biomass data, or other relevant data, and let it rip. (But see Schramski et al. 2015 for a possible general trophic model).

Howard Odum believed in the generality of systems, including ecosystems. He developed a series of "minimodels" which are still quite useful and interesting. They can be accessed today through his book "Modeling for All Scales" which comes with a CD with some generic models. Mark Brown and Dan Campbell have the most complete set of models. Mark suggests the url: https://cep.ees.ufl.edu/emergy/resources/models.shtml which has several different versions for Mac or Windows or EXCEL. A really fun and educational introduction to his modeling is to go to the web site of Lee Arnold: Https://www.youtube.com/user/leearnold. I wish it could be used much more in teaching.

Limits to Growth

At that time, meaning the 1960s and 1970s, another ecologist, Paul Ehrlich, generated a great deal of attention with his book “The Population Bomb”. Meanwhile Jay Forrester at MIT was developing a series of remarkable models that are perhaps best summarized as “The counterintuitive nature of social systems”. He developed models on business dynamics, urban dynamics, and world dynamics which showed through various feedbacks and processes that what might appear to be logical approaches to solving various problems (such as providing cheap inner-city housing) would, in his models at least, generate system behaviors that would undermine the objective of the original action. These remain remarkable and insightful studies today. He passed on “World Dynamics” to his students Donella and Dennis Meadows, Joergen Randers, and William Behrens, who, with the financial help of a group of concerned Italian Industrialists (The Club of Rome), generated a very clever and influential book “*The Limits to Growth*” (LTG) which generated extraordinary interest. This book predicted that if certain steps were not taken that the global economy and civilization itself was, after a period of extended growth, likely to experience some very rough sledding due to the combined impacts of pollutants and resource depletion.

The WORLD2 model mapped important interrelationships among world population, industrial production, pollution, resources, and food. The model showed a collapse of the world socioeconomic system and human population sometime during the twenty-first century, if steps were not taken to lessen the demands on the earth’s carrying capacity. The model was also used to identify policy changes capable of moving the global system to a fairly high-quality state that is sustainable far into the future. Undertaking the seemingly logical thing, that is investing further in resource exploitation, caused greater chaos sooner. Interestingly the *only* way that the authors of the LTG could find to generate a stable future, in which the population and other factors would not eventually move into violent changes, was by limiting the growth of the human population AND limiting all investments. If investments were not curtailed then even if the human populations were stabilized the model predicted an eventual “crash” of civilization, as spreading per capita affluence continued or even accelerated the processes of depletion and pollution generation. This is an extremely important issue not usually considered by those today devising “sustainable futures.”

From the outset, World Dynamics and especially “Limits to Growth” drew an enormous amount of attention. With the attention given to the Limits to Growth, the increasing set of “environmental crises,” and especially the “oil crises” of 1973 and 1979 there certainly was a sense among many that the LTG models were basically correct and that systems ecology writ large would become extremely important into the future.

Next, we consider the more general development of Systems Ecology.

The Search for General Principles: Natural Selection, Complexity, Self-Design and Maximum Power

Systems Ecology was not only about modeling but the search for general systems principles. I summarize some of these below. For example, systems theory has at various times been rather interested in whether systems have some kind of goal or objective. This is very much related to cybernetic concepts, such as "attractor points" that tend to generate stability, after all there is a great deal of selection for autopilots that keep the airplanes doing what they are supposed to and against those that do not. So some philosophical practitioners ask whether this concept, easily programmed into cybernetic systems by engineers, is found in other, natural, systems. This was readily understood by biologists who are very much influenced by the concept of natural selection, which might be thought of as selection for the ability of an organism to track its environment. Since there seemed to be a certain "balance" in nature, or at least a certain similarity season after season (generally), many ecologists sought for explanations in systems theory developed elsewhere, in ecosystem studies and in cybernetics (Odum with Pigeon 1970; Hagen 1992; Golley 1993).

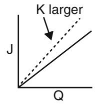
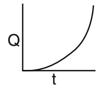
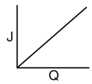
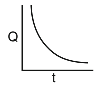
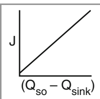
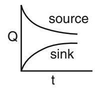
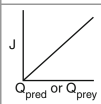
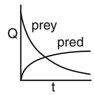
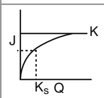
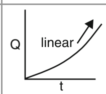
General Systems Theory

An important component of Systems thinking is that all systems share some basic behaviors (Von Bertalanffy 1968). The normal way that applied equations are taught is discipline by discipline. In principle, one would instead teach general equations and then apply them to all the different situations and even disciplines to which they apply. My favorite example is this: I was taught Ohm's law, Ficke's law of diffusion, Fourier's law of heat transfer, and D'Arcy's law of ground water flow with different equations and different Greek symbols in various different courses in graduate school. Yet all of the equations are of the same form: Flow equals some parameter of permeability times a difference in pressure in front of and behind the permeable substance. There is just one equation that took care of all these different situations. I would teach in my Systems Ecology course the equation:

$$J = k\,(Q1 - Q2)$$

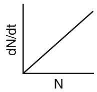
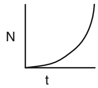
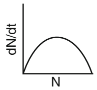
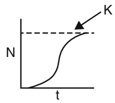
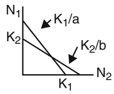
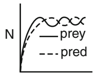
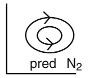
Where J was flow, Q was "quantity" (or more properly pressure) upstream and downstream from the flow, and could be electromotive force, oxygen concentration, temperature, or elevation. k was permeability (or 1/resistance). The basic equation, once put into similar units, was the same for all these different disciplines. This concept turned out to be very general, and I found that it was also very much the case for other basic equations in very different disciplines – put them in the same format (usually without Greek letters) and many things turned out to be the same basic equation. In my class, I would teach that 80% of the math that you needed for modeling was contained on two pages (Table 2).

Table 2 ***Material or Energy Transfer Equations (revised)*** This is an attempt to summarize some of the most important equations (in ecology) that are commonly used to model relations. Q = quantity of state variable; k = transfer coefficient: J = flow = dQ/dt. There are two serious flaws. (1) Nature is not that simple; (2) description is not-necessarily equality. These curves DESCRIBE functions, they do not explain them, therefore use caution with respect to these points

Common name	Equation	Shape of dN/dt vs. N	Simplest numerical "solution"	Analytic solution (where known)	Shape of solution (with line)	Uses (biological examples)
Linear transfer (source dependent) or proportionality constant	J = k*Q		$Q_{t-1} = Q_t + J\Delta t$	$Q_t = Q_0 * e^{kj}$		Source-dependent transfer, exponential growth of an organism
Special case of above: linear transfer (k negative)	J = k*Q		Same as la but J subtracted from Q			Decay of leaves, metabolism of starved poikilotherm
Linear transfer: k may vary according to conditions (often between 0 and 1) to give flow or process as proportion of maximum. For example: $PSY = k1*k2*PSY_{max}$, where k1 and k2 are dimensionless coefficients and vary from 0 to 1 to represent limiting sunlight and nutrients						Models of PSY
Linear transfer (source and sink dependent)	$J = k^* (Q_{so} - Q_{sink})$		Same but J + to sink – from source			
Feeding transfer	$J = k^*Q_{pd} * Q_{py}$		Same but J + to predator – from prey	One of many possibilities →		Transfer of heat from organism to environment
Michaelis-Menten	$J = J_{max}^* (Q/K_s + Q))$		Same as la			Enzyme kinetics, response PSY to limiting nutrient

Population Equations

N refers to numbers of a population; N_1 and N_2 refer to different populations. Note that many of these curves and formulas are similar to those above. It is generally better to use life table/physical analysis but you should know these.

Class	Common name	Equation	Shape of dN/dt vs. N	Simplest numerical "solution"	Analytic solution (where known)	Shape of solution (with line)	Uses (biological examples)
A	Population growth (exponential)	$dN/dt = rN$		$N_{t+1} = N_t + tN_t\ \Delta t$	$N_t = N_0e^{rt}$		Population growth in unlimited environment
B	Population growth (logistic) also described by →	$dN/dt = Nr((KN)/K)$ $dN/dt = aN-bN_2$		$N_{t+1} = N_t + N_tr((K-N)/K)t$	$N(T) = (Ke^{rt}N_0)/K \div (e^{(rt-1)}N_0)$		Self-crowding, K = "carrying capacity"
C	Population growth (logistic with competition (Gause Model))	$dN_1/dt = r_1N_1((K_1-N_1-aN_2)/K_1)$ $dN_2/dt = r_2N_2((K_2-N_2-bN_1)/K_2)$		$NI_{t-1} = N_{t1}$ ÷ all that			a = per capita equivalence in crowding of N_2 on N_1
D	Population growth (with predation) (Lotka Volterra)	$dN_2/dt = r_1N_1 + a_1N_1N_2$ $dN_2/dt = r_2N_2 - a_2N_1N_2$		$N2_{t+1} = N_{t2}$ + all that			$a_1N_1N_2$ = pred. Rate $a_2N_1N_2$ = assim. rate

The concept of the generality of equations, or at least their data, guided me in my first three papers published in Nature and Science, when I took concepts from one discipline and applied them to another. These were: (1) a metabolic analysis of the wiggles in the Mauna Loa curve of atmospheric carbon dioxide using procedures I had learned in stream ecology (the annual CO_2 wiggles looked like the daily fluctuations in stream oxygen) (e.g., Hall 1972; Hall et al. 1975). (2) an examination of data from the US industry using techniques, I had been teaching in fisheries analysis (Hall and Cleveland 1981). This research was reported on the front page of the Wall Street Journal! (3) And finally, I have gained my modest claim to fame by applying the concept of Energy Return on Investment (EROI) that I had derived in my doctoral work on fish migration (Hall 1972) to looking for oil (Hall and Cleveland 1981; Hall et al. 2014), and eventually to a general examination of economics (e.g., Cleveland et al. 1984; Hall and Klitgaard 2017; Hall and Klitgaard 2019). Hence, I would say that there is a lot to be gained by keeping your eyes open if you move from discipline to discipline as I did, to see if there might be something well understood in one discipline that could be applied to another. Whether this can be taught or not is a more open question, but I think this is an important component of graduate training.

Complexity

Natural ecosystems are almost bewildering in their complexity, especially if one focuses on the different species. In the 1970s, especially within the IBP, there was a great push to make ecosystem models more and more complex by measuring and adding in more species and by generating computer algorithms that could deal with this increased complexity (Coleman et al. 2004). More generally, there was a sense that systems science could be made better by understanding and modeling complexity as its own entity. I can remember one researcher at a meeting saying that for one of the IBP models they had 3000 species in their ecosystem. For these they had time series data on abundance for 500 of them, some data for another 1000 and none at all for the remaining 1500. Other modelers, such as Howard Odum, paid relatively little attention to all the species but focused on trophic levels or occasionally functional groups. Today there is a lot of attention paid to species diversity, but not much to trying to include all species into models. For example, Robert Ulanowicz is known for studying the complexity of food webs (e.g., Ulanowicz 1997), and Neo Martinez for examining the structural relation of the species with different ecosystems (e.g., Martinez et al. 2006). There is a related very rich literature in ecology examining the relation of species diversity to various systems attributes, such as stability (defined in various ways), but that literature is too vast, complex, and, in my opinion, inconclusive to merit much attention here (e.g., Goodman 1975; Strong 1986). Something simple but useful that, to my mind at least, derives from complexity "theory" is that in real systems, including biological and social systems, there may be many causative agents when the human mind seems to be formed to seek a single explanation. Thus a hurricane or a population crash in nature or a stock market crash may have not one but many causes. The elusive holy grail of much of modeling is to try to understand and represent the system well enough to allow such multiple agents to indeed determine the system being modeled. Dan Botkin (1977) wrote a paper I liked where he had a section: "in praise of medium-sized models" where he extolled the utility of not the necessarily simple (few starting equations) analytic models nor the thousand species complexity but something of modest size. I think this is good advice, even if difficult to nail down precisely.

Cybernetics

Norbert Wiener (1894–1964) defined cybernetics in 1948 as "the scientific study of control and communication in the animal and the machine." The concept spread rapidly in the physical sciences (see Chapters 2,3,4) and in some aspects of biology. It was picked up in ecology mostly by ecologists who were interested in finding a way to quantify in some way biodiversity. In a number of papers, species were used as units of diversity, and the diversity of communities of species were assessed in terms of Shannon-Wiener information theory. Exactly why species should be the units of diversity is not quite clear and has not been argued other than the data is readily at hand. For example, different life stages are often completely different entities and all species that eat grass have maybe more in common than one would think by their being different species. As an independent effort the diversity of trophic pathways in ecosystems was assessed by Patten (1959). The concept has continued through today (Pennekamp et al. 2018). Howard Odum (e.g., 1983) was also very interested in the relation of feedback controls to ecosystem processes and stability, although he thought more in terms of nutrients limiting productivity more than diversity of species generating stability. Recent reviews of the meaning of information is given in papers by Lombardi et al. (2016), Lombardi and López (2018), but all such definitions remain for me far from intuitive.

The concept of feedback is important to both cybernetics and models in ecology (Holling 1973). Fundamentally, the concept is that if one has a target (a direction or a desired level of some component or characteristic of an ecosystem), and if one has a sensor and an operator that generates a *negative feedback*, that is a change in direction that brings one back towards the target, then you have some kind of basic cybernetic system. Another, more formal, definition, was offered by Pat Lane "feedback is the effect of a variable on itself by way of intervening variables." The obvious example is learning to ride a bicycle: if you are wanting to go in a straight line, then if your bicycle is aimed too far right then turning the front wheel toward the left will bring you back towards the desired direction – as long as you do not do it too much!

Early models in ecology often focused on the supposed stability of many wild populations: if the number of deer or grouse increased above a "carrying capacity" (known as K) during a good breeding year then (in, for example, the logistic equation) various kinds of "density dependent" relations, such as ease of spread of disease or concentration of predators, would kick in and bring the population towards the carrying capacity. And the converse. Another famous example was for Canadian hares and lynx, based on extensive records of pelts delivered to the Hudson Bay trading post at Hudson Bay. The data for these animals cycled again and again with the lynx slightly behind the hares in many large but regular fluctuations. The mathematics that had been derived to represent these stabilizing processes (lynx eating more hares when they were more abundant and the converse) were simple and appealing and looked superficially like the data, and led to a great many papers with often complex mathematical elaborations but usually with very little empirical validation. These were great stories and allowed many to see nature as very much on the ball with respect to regulation and stability.

Unfortunately animals in nature are very difficult to census, and many of the supposed good examples were shown to be more the imagination of ecologists than reality (Hall 1988). For example, sometimes the increase in lynx preceded that of hares in their cycles – which by the logic of the equations made sense only if hares ate lynx, and the pelts were not even from the same region: the hares were from more local sources and the more valuable lynx pelts tended to be shipped to the Hudson Bay post from Western Canada. In other words, they were not particularly overlapping populations. And hares on Anacostia Island, where there was no lynx, cycled anyway. There were many examples in all the ecology textbooks (many still) including Kaibab deer, Argentinian ant lions, and so on. The few (often false) "examples" were passed on from one textbook to another, generally without comment even after their dubious, inappropriate and sometimes fallacious nature had been clearly exposed (Hall 1988; Meistera et al. 2018). Nevertheless, there is a certain stability in much of nature that we barely understand. For example, in the Luquillo forest of Puerto Rico frogs, birds, and walking sticks seem to have returned to pre-hurricane levels following large changes associated with the passage of hurricanes (Willig et al. 2019). The populations were very susceptible to large changes in external forcings, but also had some kind of stability.

The appeal of the supposed self-regulation of animal populations led to a cottage industry of mathematical ecologists, sometimes theoretical and sometimes applied, trying to regulate actual populations in supposed need of regulation, such as game animals or exploited fish (Goodman 1982, 1987). For example, using the Ricker curve, a derivative of the logistic (of carrying capacity fame) led to the concept of "surplus" spawning populations (often greater than half the spawning stock) and gave mathematical sanctioning to the continual overharvesting of salmon and other fish. The truth was revealed by empirical analyses of, e.g., Downing and Plante (2011) which showed that essentially every fish population they examined that experienced a harvest of greater than 10% of its spawning population declined and/or went extinct. Meanwhile ecosystem-level (vs. population-level) studies frequently found that periodic changes in, e.g., climatic forcing or the physical properties of water columns and or other regulators of plant production were more important in determining the strength of spawning and hence subsequent populations (e.g., Hjort 1914; Sharp 1991). And of course, more generally overfishing has enormously impacted fish populations (e.g., Worm et al. 2009).

But the concept of self-regulation and the importance of biodiversity in maintaining community homeostasis has continued to exist within the discipline of ecology with occasional studies lending it support (e.g., Tilman 1990; Lehman and Tilman 2000; Willig et al. 2019). The concept seems so intuitive (e.g., Odum 1964; Woodwell and Smith 1969) and supplies such an excellent logic to biodiversity protection that whether it operates routinely or not, it continues to have great impact in ecology. At the extreme, we all know that "the random walk eventually falls off the table" and in the absence of human intervention or climatic events outside the "normal," nature in general, and even species, rarely goes extinct or increases without limit. Surely there is some kind of regulation, even if it operates only at the extremes. Hutchinson (1959) set the stage for later discussions by saying that vegetation was limited by incoming sunlight, and upper trophic levels by the 10% (or so) transfer of the solar energy at each step, and that species could not overlap in size by too much. Hairston et al. (1960) wrote a famous paper stating that "the world was green" (i.e., not grazed down to the nubbins –although prairie grasses might take exception), which they attributed to predators controlling herbivores to levels lower than where they would overgraze. Later Whittaker and Feeny (1971) built a more convincing case based on plants defending themselves with "secondary" chemicals (turpines, mustard oils, alkaloids, silicas, tannins, nicitoids, various narcotics) and the like whose business was to discourage herbivores. While caffeine, mustards and THC might be interesting dietary supplements to our own lives, they would hardly do for a steady diet. Donald Strong (1986) summarized the various often contradictory population studies by summarizing the relations as normally "density vague". There were many responses pro and con. That is probably where we are today, with little information of routine density dependence but some indication that it works sometimes, if usually at extremes in population levels (Pennekamp et al. 2018).

My own sense of what controls ecosystems and populations, derived while working on plankton models of the North Pacific and of Flathead Lake and plant distribution in Puerto Rico, was that plant and animal populations were much more determined by the resources available, and their cost of exploitation. The relation between costs and gains allow (or not) existence, growth and reproduction. This was most explicitly energy costs and gains from living at different places on the landscape and as this relation changed from one year (or time period) to another (Hall et al. 1992; Harris et al. 2013). Thus every organism is controlled by the environmental conditions of their micro or meso location (and this can include biotic factors such as predation, parasitism, disease and competition) and I have developed this concept in terms of energy costs and gains along environmental gradients (Hall et al. 1992; Hall 2017a).

Related to this is my sense that Le Chatelier's equation has been greatly underappreciated in ecology (while researching this paper I found the same statement from Chernyshenko 2008). Le Chatelier's principle is summarized with the simple equation:

$$A + B \longleftrightarrow C + D$$

where the letters refer to concentrations (or "pressures") of various reactants and products. The double arrow means that the reaction will go in the direction of less concentrated products until equilibrium is met, but that if the equilibrium is upset then the reaction will go on average in the direction that will tend to restore equilibrium. Hence if A is the concentration of elemental phosphorus in the water and B the phosphorus in inorganic dissolved salts, then if the growth of phytoplankton removes phosphorus it then becomes sequestered in the biotic phytoplankton C and the zooplankton D. The sum of A + B + C + D is a constant, at least (neglecting sinking) until the water mixes in the winter. Thus as the biotic concentrations increase, the inorganic forms are depleted and the growth of the phytoplankton is increasingly restricted until the energy cost of concentrating phosphorus from a very dilute environment costs the plant more than it can gain from its incorporation. As the concentrations of C + D increase more will pass back to A + B, in turn allowing a bit more growth. The point is that the physical availability of nutrients is a large regulator of the growth and biomass of an ecosystem. But the faster the system grows the more quickly it becomes nutrient-restricted. Of course if some external event increases the nutrients (or energy supply if energy is modeled) the ecosystem can expand. This continues as long as the ecosystem is not disturbed.

Howard Odum (1983) suggests that most or at least many ecosystems tend to be "pulsed" at regular or irregular intervals such as once in a hundred (or million) year floods, hurricanes, fires and so on. Indeed he says that they are selected to withstand and recover from these pulses, which are in fact essential for maintaining long term productivity. Hurricanes in the Luquillo forest of Puerto Rico seem to be a good example.

Meeting Cybernetics and Raising You One: Self-Design

A number of systems scientists have become interested in apparent "self-design" (sometimes called self-organization) of many systems. The first example was probably Ludwig Von Bertalanffy (1901–1972), originally an embryologist. A very interesting phenomena in embryology is that a fertilized egg (or blastula) of an embryo will grow by dividing into two, four, sixteen, and so on cells. If you divide the embryo into half at 2,4, 8, or 16 cells each part will grow into a complete frog! The complete information to "self-design" a frog is within each cell. We would say today that each has a full complement of DNA.

Howard Odum believed that self-design operated through natural selection at the level of individual organisms, organism-to-organism transformations, and ecosystems (Odum and Pinkerton 1955; Hall 1995b; Brown and Hall 2004). Any energy surpluses garnered by an organism would generate selection for new organisms by means of preservation of useful energy which would be utilized for growth and reproduction. At the level of the complete ecosystem, any surplus energy garnered by the system-wide energy pathways was utilized to increase the biomass associated with that pathway and displace other competing pathways (Lotka 1922a, b, 1924). All of this would be influenced for selection for "maximum power". According to the maximum power principle, there would not be natural selection for maximum efficiency or maximum rate for many biological (and other) processes, but rather for intermediate rates of any one process. This would optimize the tradeoff that often occurs between rate and efficiency of exploitation. Odum extended this concept to a more comprehensive view of eco- and other systems being selected through self-design for capturing a maximum amount of energy available. While Odum was sometimes criticized for being teleological and also for believing that there was natural selection within human economies for grabbing all the power possible, a careful reading of his papers shows that he was a very strong Darwinist, although we may wish to say Darwinism writ large, and that he was essentially apolitical in his perspective.

Probably the ultimate place this idea was taken was by Odum (1983) with his concept that many systems were self-designed for capturing the most energy possible, that they would take such energy as they had and use it to generate structures and processes that would capture even more energy. One of his (and others) first examples is the Bernard Cell, a large Petri dish of inorganic salts. When heated by a Bunsen burner it generated cycling structures of the fluid salt which would capture even more of the heat of the Bunsen burner. Odum applied this ideas to ecosystems through succession and evolution. A bare field will not stay bare or a small lake will not stay in that configuration indefinitely, but through succession (a more or less orderly transition of plant (and animal) species in an ecosystem through time) develop more structure until the "climax" vegetation is reached, which normally is more or less the maximum biomass and productivity that the climate and energy input can maintain. This is perhaps not so different from the view of most ecologists. But Odum took it a bit further – he believed that ecosystems, and systems more generally, would evolve toward "maximum power" where there would be natural selection for new species and new biochemistry that would enhance a maximum capture of the available energy. Somewhat similar concepts were developed from a thermodynamic perspective in various papers by Eric Schneider and James Kay (1994–1995).

A cute example is given by McClanahan and Wolfe (1993), with a tree, or any perch, that exists within a grassy field far from the forest edge, especially if it is a tree that produces fruit such as cherries that will attract birds. These birds often bring in additional tree seeds with their defecations while also fertilizing the later seedlings, all of which accelerates succession and capture of the sunlight falling on the clearing. Likewise the successional *Cecropia* trees in Puerto Rican rain forests produce considerable fruits that fruit bats like to eat. The bats roost within the forest edge but when they wake-up they circle the treeless disturbed areas, defecating (like disturbed birds) while they waken enough to negotiate the forest interior – meanwhile reseeding their favored food into the unshaded environments where they will grow most rapidly (Odum, personal communication). This evolving commensal relationship speeds the succession and possibly evolution of the ecosystem as well. He also extends the concept of self-design to maximize power with inanimate examples such as hurricanes and stars. There is no question that hurricanes are self-designed systems because they have physical structures (upwelling processes in their center) that extract heat from the ocean which accelerated their power as long as they stay over warm waters.

Systems Ecology: What Are We Left with 50 Years Later?

Today we are surrounded by, immersed in, besieged by, various computer models in all of our electronic gadgetry, most of it run on some kind of programming. Ecology as a concept, or at least a term, is certainly far more extant, obvious and influential even as it has been expropriated and often watered down by all manner of applications unimagined by its originators and practitioners of half a century ago. But that is hardly Systems Ecology. Systems applications today has become mostly the replacement of mechanical-servo mechanisms with electronic systems to do more or less the same function, although often in a much more complex way, and the use of “ecology” is, well, diverse. So, for the former it is necessary to differentiate these conceptually limited systems designed to do a specific (although sometimes complicated) task from some kind of truly “systems” activity, which is not easy and is perhaps very subjective. I am not too aware of too much real “systems” teaching in our universities today, although I hope I am wrong. The half dozen reviewers acknowledged below do not explicitly disagree, at least from the perspective of general programs. As the students of our great initiators and innovators progressively retire so did most formal graduate programs in systems ecology. Exceptions include the International Institute for Applied Systems Analysis (IIASA) in Austria, and various programs in the United States and elsewhere (University of Montana, for example, has a program called Systems Ecology with a focus on ecosystems) devoted to some particular aspect of ecology, but without using the name explicitly, although as noted in sections below strong spinoffs continue today in various Environmental, Energy and Ecological programs. I do have the sense that real quantitative analysis in ecology, other than those based on counting species, is far less than it used to be. But there is also a great deal of complex computer modeling in related activities, such as climate change and the examination and mapping of species distribution and sometimes loss. And there are good ecologists who believe that the best models are not complex simulations but simply correlations amongst interesting variables (e.g., Peters 1991).

Initially (meaning in the 1960–1980s) there was a great deal of excitement and hope that the systems approach would lead to a series of good predictors of the future, and this would lead decision makers to understand and appreciate the "limits to growth" and the need to model human society increasingly after natural ecosystems. What actually took place is quite a bit more modest than our expectations. Ecology continues as a viable academic discipline and still inspires many young people. But ecology as a discipline, once unified to some degree by Gene Odum's textbook, *Fundamentals of Ecology* (1953, 1st edition), has become somewhat disjointed in focus: one path investigating mostly biological issues of species, populations, communities, evolution, and conservation ecology; and, a second focusing on the more holistic approach of ecosystems, energy flows, and material cycling, more often including humans as a component of the ecosystem being examined and sometimes with direct application to issues relating to the depletion and despoliation of energy, key materials, species, and ecosystems. Climate, sustainability and conservation issues have taken center stage. While humanity is enormously more aware of, and sometimes sensitive to, the environment compared to those original years, Systems Ecology as a discipline, with some notable exceptions, has had little influence in directing how we live on this planet except perhaps adding to the understanding of the processes of nature (and their disturbance) that have and are taking place.

As for Systems Ecology as a discipline most of the students of the pioneers (the Odums, Patten, Holling, Watt) have retired or are approaching retirement. Clearly the first "pioneer" generation set the standard in terms of generating literature and students, and the second generation pretty much maintained the productivity, if not the originality, of the first. Considerable work continues by the third generation in specific societies and Journals associated with subdisciplines spawned by Systems Ecology (Ecological Engineering, Ecological Economics, BioPhysical Economics, Estuarine Ecology, Emergy analysis, Holling's Resilience Alliance) but the main ideas of Systems Ecology have been co-opted by a very interdisciplinary audience now so they are really everywhere (ideas such as resilience, EROI, ecological economics, ecosystem services, networks, etc.). But Systems Ecology as a distinct discipline does not seem to have very much explicit structure anymore. Probably Howard Odum would not be displeased, as he believed strongly in putting out lots of ideas and let natural selection take its course as the academic and physical environments changed.

Specific Models that Are Still Being Used in Ecology

I am rather hard pressed to find too many models that were developed back in the initial days of Systems Ecology that are being used now, although in a limited sense the modeling concepts derived from them are widespread. But there are some explicit exceptions. Steve Running supplied the following pertaining to the original IBP work. He thought two early models are still being used routinely:

"The International Biological Program was active basically in the decade of the 1970s. This program spawned most of the first generation of ecosystem modeling in the United States. The models of the time were highly computationally limited, yet attempted to be comprehensive in their treatment of the ecosystem of interest by having high parametrization demands. As such few survive until today in any form. However, there have been some exceptions, ecosystem models that pursued elegant simplification and that continued to evolve, led by active ecosystem modelers. I list below several early systems models are operating today in some form, 40 years later.

The Deciduous Forest Biome, headquartered at the Oak Ridge DOE National Lab gave rise to the FORET family of forest ecosystem models. These models derived their original logic from the JABOWA model of ecologist Dan Botkin and several investigators at IBM, and Hank Shugart and colleagues derived many variants over many years. These models simulated the growth of different trees of different species competing for light and other resources in a 0.1 ha plot, as controlled particularly by canopy light competition. The ED or Ecosystem Dynamics model led by Steve Pacala is a recent example of this modeling family.

The Grasslands Biome was headquartered at Colorado State University, and modelers Bob Woodmansee, George Ennis, and Bill Parton developed CENTURY in 1978, a grassland model that focused on soil biogeochemistry and decomposition processes. A newer, daily time step version of this model DAYCENT is still actively used and incorporated agricultural management practices, so has both theoretical and practical value.

The Coniferous Forest Biome was co-led by University of Washington and Oregon State University. Their early model CONIFER was abandoned in the 1980s, but the modeling of Steve Running, beginning with a simple tree water balance model H20TRANS in 1975, was expanded to FOREST-BGC in 1988 and generalized to BIOME-BGC in 1991, and is still used by ecosystem modeling teams. Much of the logic in the Community Land model of the NCAR (National Center for Atmospheric Research) global climate model was brought from BIOME-BGC by Peter Thornton in the 2000s."

Bernie Patten was still using a general ecosystem model to investigating how food chains utilized trophic resources through many cycles of consumption well into the 2000s.

Various students and colleagues are using "Odum type" models to model a variety of issues although it is pretty difficult to specify any particular explicit models that have made it through the decades since the 1970s. Rather Odum's approach of using systems diagrams to delineate and formalize each particular problem, and then writing and solving equations continues in spread sheets, with the modeling program

Stella or explicit code. Probably the strongest or most coherent group is the emergy group still having biannual meetings at the University of Florida. Students of John Day have used various energy models to examine the energy intensity of maintaining humanity's desired structures in delta environments (e.g., Wiegman et al. 2018). There are many former students and colleagues throughout the world who are using Odum modeling approaches for specific problems, such as Agricultural production. For example, in Brazil Enrique Ortega is working on continuing biophysical and social analysis to try to reduce hunger (Santos and Ortega 2019).

Specific Programs that Were Spin Offs of Systems Ecology That Continue Today

Several strong Estuarine programs continue, such as those inspired by Scott Nixon at the University of Rhode Island, by John Day at Louisiana State University, by Dan Campbell at EPA and elsewhere. We had a great program in Systems Ecology at SUNY Environmental Science and Forestry, with many graduate students and many publications, but with my retirement it seems to be different or perhaps gone. This is one thing that seems the general case: it takes a strong personality to maintain a program unless there is unusual administrative support.

Limits to Growth Models

A very powerful exception to the relatively low remaining direct impact of many systems ecology models are the Limits to Growth models, as stated above. The authors have released a series of reviews and updates of the models, most explicitly Meadows et al. (2004). There have been a number of explicit tests of the original base case model and these studies conclude that despite the fact that the original objectives of the model were not to make explicit predictions, but to explore relations among variables, the track record of the model is rather good (Hall and Day 2009; Palmer and Floyd 2017; Fig. 4). The very strong oscillations predicted by that model have not occurred yet in most of the world, but if the appropriate scale is used they were not predicted yet by the model either. The lack of a y axis time scale in the original model continues to haunt us.

Petroleum and Energy Production Models

The most successful models that I have been involved with personally are probably our oil production prediction models (e.g., Hallock et al. 2004, 2014). Whether these models are "Systems Ecology" models or not, I leave up to the reader's discretion, but certainly they flow out of these modeling concepts. These models project nation by nation petroleum production using the concept of a Hubbert (bell-shaped) curve and different estimates of ultimate reserves. They were originally developed by

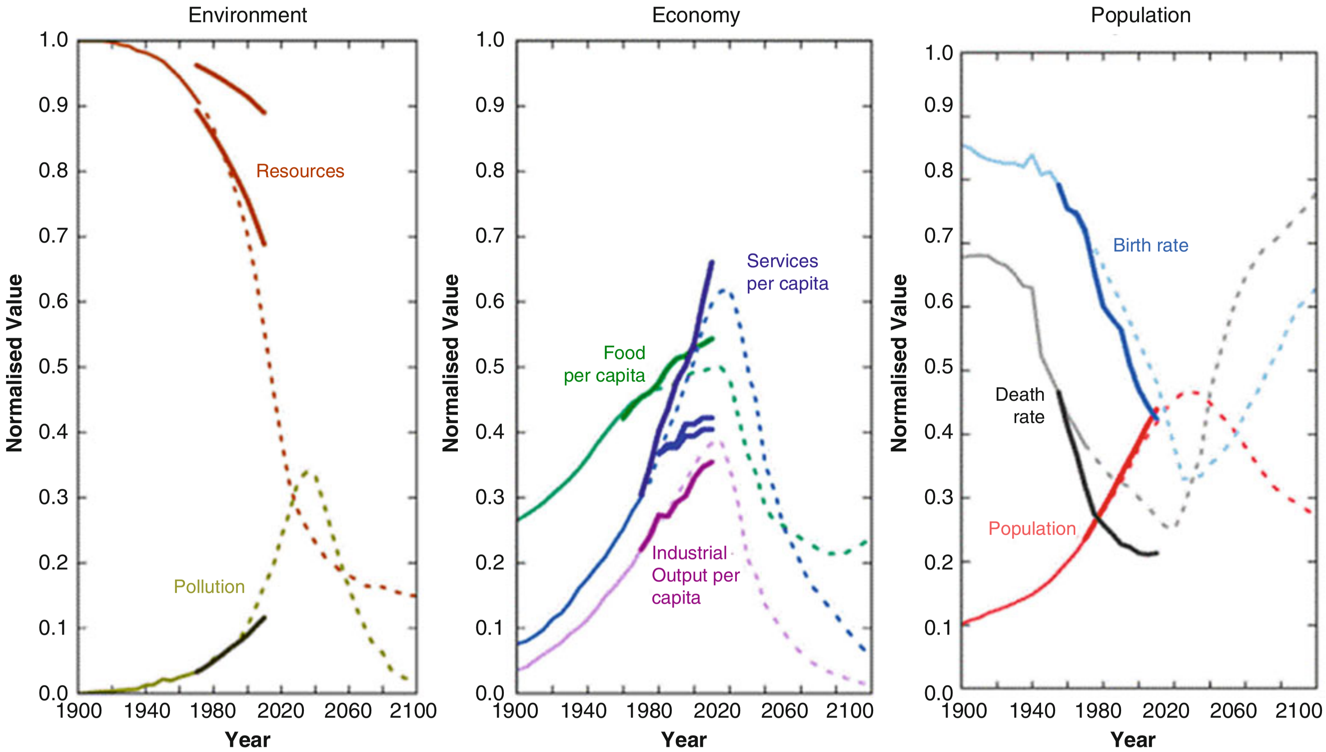


Fig. 4 Turner's comparison of the output of the limits to growth model with actual data, showing the model seems to be pretty much on track. Similar results were found by Hall and Day (2009)

myself in FORTRAN and simultaneously by my former student John Hallock on a spread sheet. Since the two approaches gave essentially the same results, and John was far more conscientious and skilled than I in trying to get the input numbers correct, I gave up the FORTRAN. The particular virtue of this approach was that we made predictions for 40 odd oil producing nations, and then came back 10 years ago to see how accurate our predictions were. The answer was quite accurate, as can be seen by the explicit nation by nation results given at the bottom of our 2014 paper! Nearly all of the smaller and medium-sized oil-producing countries followed a Hubbert curve and had already reached a clear peak by 2014. A partial failure of the model is that it was designed for conventional oil and did not predict the oil shale revolution in the United States. It also did less well (but adequate) for the very largest countries whose production was limited more by political agreement than geology.

There are a number of good academic programs that are systems oriented but more appropriately considered as energy programs: ones at the University of Leeds in the UK (e.g., Brockway et al. 2019) and at the University of Valladolid in Spain (e.g., Capellan Perez et al. 2019) stand out in my mind. The University of Canterbury in Australia has a good program focused in part on the Energy program GEMBA (Global Energy Model using a Biophysical Approach). In addition, there are individuals undertaking very good work, in my opinion, at University of Texas (King 2015), and Stanford University (Masnadi and Brandt 2017).

Ecological Economics

Ecological Economics continues to be a strong field and Journal initially developed especially by Robert Costanza, a PhD student of Howard Odum. It focuses especially on evaluating nature’s contributions to human welfare and economies and also on developing the economic basis for sustainability, but undertakes many diverse activities and has well attended meetings annually. Although the initial focus of its initiation in 1989 was in large part on the failures of conventional economics the Journal has shifted, after its initial years, to using conventional economics (i.e., money) for evaluating nature in various ways, such as ecosystems services (Melgar-Melgar and Hall 2019). A synthesis of various ways to bring more environmental and systems approaches into the teaching of economics is a special issue of the Journal Sustainablity “Advances and innovations in sustainability education” edited by Tina Evans (Forthcoming).

Biophysical Economics

A spin off of my own PhD work on fish migration, as influenced by the early Odum investigations into the relation of energy and the economy (e.g., Odum 1973, 1977) was my own development of the concept of EROI (Energy Return on Investment, e.g., Hall 1972, 2017a; Hall and Cleveland 1981; Cleveland et al. 1984; Hall et al. 2014; Court and Fizaine 2017). This has spawned a great deal of research and many papers summarized in Hall and Klitgaard 2017. A second large effort was the development of the field and discipline of BioPhysical Economics (Cleveland et al. 1984; Kummel et al. 2002; Hall et al. 2001; Hall and Klitgaard 2017). This field examines economics not as a social science, as is usually the case, but as equally a natural science where economic production and distribution is a biophysical process dependent principally on energy and material flow. It is very critical of the field of conventional (i.e., neoclassical) economics, and believes that in the long run we can understand economies much better by including a biophysical base (Sharp and Hall 1995; Hall et al. 2001; Hall and Klitgaard 2019; Melgar-Melgar and Hall 2019). The International Society of BioPhysical Economics has well-attended meetings more or less annually. The Journal BioPhysical Economics and Resource Quality publishes many pertinent and excellent papers. See http://isbpe.org/index.php/en/ or search for BioPhysical Economics. A separate but affiliated BioPhysical Economics Institute, with a much closer relation to corporations and financial investment strategy, is being developed at press time (see www.bpeinstitute.org).

Emergy Analysis

EMergy (Energy memory) analysis, developed by Howard Odum in his later years, and carried forth since his death in 2002 by Mark Brown, Sergio Ulgaldi, and many others, attempts to examine all of the energy flows, including the various energy flows of nature, that enter into the process of economic production. Their main argument is that, e.g., most energy analysis considers only the flows of fossil energy that are used to, e.g., support economies and do many things. They beleive that it is important to include all the flows of energy (e.g., the solar energy required to generate the rain required to grow a crop or make an automobile) and this involves a fairly complex analytical process, which they have clearly specified (e.g., Odum 1996). Emergy analysis has very strong advocates and practitioners led by Mark Brown and Sergio Ulgaldi. They have annual meetings and a very dedicated core membership (see Emergy Society (https://www.emergysociety.com/).

More Subtle Influences

There has been much more impact on today's collective thinking and decision making from the newer disciplines of climate change, biodiversity conservation, and energy analysis, which are related to systems ecology only indirectly. Within these disciplines, a less formal systems approach and certainly modeling remain important and powerful for dealing with many explicit issues. But it would be a stretch to trace these approaches back directly to the original systems ecology. Nevertheless given the enormous and complicated problems humans face with climate, energy, species management and conservation, human health, and so on, it is clear that a systems approach has a great deal to offer. In fact, some kind of a systems approach is used routinely in many of these issues (e.g., simulation modeling in health studies (Stewart Ibarra et al. 2013, 2014), toxicology (Dixon 2012), land use change studies (Pontius et al. 2017; Ustaoglu et al. 2019), and many concepts of sustainability). So, in a sense, systems ecology has become routine, even if not so named. If the economic system, writ large, has not been especially affected, the management of many of the subcomponents are influenced by a systems approach.

Probably the most important legacy, within ecology anyway, of all these earlier modeling efforts from the 1960s–1970s was to generate a view of the legitimacy and importance of understanding nature at the ecosystems level. While very many models were made of specific ecosystems and specific questions, curiously there does not seem to be very many computer models that were passed on to be used by future generations of ecologists, in part because the difficult part was not conceptualizing and modeling the trophic or (other) stocks and flows but rather understanding the determinant relations and getting the data to construct a parameterized model.

Perhaps a conceptual grandchild of their efforts, and the first-generalized trophic model that I am aware of is Schramski et al. (2015). It seems that such a model should have been the product of one of the above efforts but I am not aware that it is. On the other hand, we are left with the general conception of complex ecosystems as an entity worthy of study, and the beginning of the ecosystem – level concern about the general degradation of ecosystems is clearly a modern-day inheritance of those early icons.

Meanwhile the questions raised by the early systems scientists and ecologists, including the problems associated with attempting to generate indefinite growth in a finite world, remain – and are enormously exacerbated. The population issue still underlies all problems (Ehrlich and Ehrlich 2016), oil remains precarious (Hall 2017b), species are being assaulted from all angles and we are besieged with studies that suggest that civilization is in a very precarious position (e.g., Rockström et al. 2009, Ahmed 2017; Bardi 2019). It seems that while the wolf has been delayed, it remains at our doorstep, exacerbated by the relatively new arrival of potential climate change.

Some Things I Think I Have Learned About Systems Thinking and Modeling

Much of what I learned about systems science 50 years ago was focused on complexity: conceptual complexity, mathematical complexity, and diagrammatic complexity. What survives in my own mind now is much simpler, although I do not know if it can be learned without going through all the complexity steps. Here are the most important principles of systems science in my mind today:

1. While systems are by their very nature and definition complex, there is an underlying similar pattern to all, or most, of them. Once you become familiar with the general pattern you see it again and again and again.

2. Although each system, be it ecological, economic, social or engineering, while often enormously complex in its details, usually can be understood best by simplifying into perhaps a half dozen to dozen major components.
3. These components include not just the major units of the system of interest, aggregated into super categories, but also the forcing functions from outside the system. These usually include structures to capture, store, use for selective advantage and hence to dissipate the incoming energy. There are evolutionary principles at work here (Hall 2017a, b).
4. It is very useful to start with a complete energy budget, from sources to storages to ultimate dissipation for, in my opinion, energy is key to understanding systems. More generally, energy and its relation to organisms' metabolism is a key part of understanding biology (e.g., Brown et al. 2017).
5. It is always good to diagram the system and its important parts, identifying the boundaries, and the components listed in three above.
6. An especially important part of the conceptual/diagrammatic modeling is locating "work gates", that is junctures in the process where a relatively small unit of energy influences the flow or behavior of a larger component. (For example, the small amount of energy that regulates the flow of large amounts of water through a dam or penstock, or for a plant the energy used to exploit phosphorus in the soil.) This may lead to important leverages for management or regulation of impacts.
7. Most ecosystems, including human dominated ones, will have the same basic components, listed here as their ecological types: Energy sources, primary energy capturers, downstream storages and consumers, work gates.
8. It is much easier to simulate most physical entities than biotic entities. For example, it is much easier to simulate approximately the daily and seasonal solar inputs and even the photosynthetic response than the year to year variation in reproduction of the same plants. Thus one good way to model ecosystems is to start with understanding and simulating the seasonal physical entities, such as sunlight, rain and temperature (including the statistical variation).
9. Models that are strongly forced by external events are usually more accurate than models that depend upon interior machinations.
10. 8 above also means that my own models of physical processes clearly have been more successful than biological ones (e.g., modeling of oil production for some 40 countries vs. biological populations (Hallock et al. 2014 vs. Levitan and Hall in preparation).
11. Probably the most critical, difficult and useful steps in modeling are the original development of the conceptual/diagrammatic model and the eventual use of validation and sensitivity analysis.
12. A great deal of time and effort have been wasted in ecology developing over mathematized theoretical models without validation in nature. An important question is to what degree, or even whether, useful theory in ecology can be derived from mathematics alone vs. observation and measurements in real ecosystems. Egler (1986) writes of "Physics Envy in Ecology" (pun intended), where she accuses ecologists of seeking to emulate the power that mathematical

models have had in physics (but where physical systems are often simple and real ecosystems much more complex).

Teaching Systems Ecology

Many of us "second generation" systems ecologists taught systems ecology in one form or another over the past 50 years. Since it is clear that the need for a systems approach to the world's problems is not going away, but also that the support for such positions within academia is uncertain at best, and that much of what we had learned about teaching systems ecology was in danger of being lost forever, several of us organized a special edition of the Journal Ecological Modeling (Hall et al. 2017a) with a series of papers by people who had been teaching Systems Ecology or modeling in some way. There are several sources of teaching materials, including the early chapters from Hall and Day (1977), DeAngelis (2010), Odum and Odum (2000), Meadows (2008), Montague (2014), Jorgensen (2012) and the material from Lee Arnold mentioned above.

For example, some of my students and I have a paper summarizing my approach, which is to teach systems ecology starting with nature rather than textbooks or equations. In this approach the students start by going out the first weekend of the fall semester and camp on a lovely small trout stream where they, organized into teams along a semi-military hierarchy (with general Hall, lieutenant physical, lieutenant benthic insects and so on, quartermasters, cooks and so on) to measure the flow of energy from the sun to the plants to the insects to the fish to the kingfisher. The students would also undertake a series of experiments to determine the abundance and metabolism of individual components, such as the metabolic response of different sized fish to different experimentally-induced water temperatures. Then the students would learn to organize their data in computer files and build a series of increasingly complex models based on the data they collected themselves. The details and the results of one year's analysis are given in Hall et al. (2017b). I used this approach to teach about 800 enthusiastic and even grateful students in Systems Ecology over some 40 years, many, many of whom went on to distinguished (usually applied but using systems, modeling etc.) careers. The amazing and diverse applications of my own more recent graduate students can be seen at: https://www.dropbox.com/sh/jw87t36j6xdqmx2/AADI1xbE4BFGvApPDM3bx2sFa?dl=0. There are also many other good papers in this special issue.

Conclusion

While there seems to be little interest or understanding of these issues today, especially at the level of University or Departmental administration, except among a few dedicated analysts, writers and the general public, depletion and degradation of resources continues unabated and by many accounts has accelerated (e.g., Rockström et al. 2009). The fundamental issue as to whether civilization is doomed or not continues unabated (for one recent example see the paper by Ted Nordhaus "The Earth's carrying capacity for human life is not fixed" aeon newsletter https://aeon.co/ideas/the-earths-carrying-capacity-for-human-life-is-not-fixed and the response by Richard Heinberg "Ted Nordhaus Is Wrong: We Are Exceeding Earth's Carrying Capacity" https://undark.org/article/ted-nordhaus-carrying-capacity-ecology/).

My own perspective is that the issues and basic approach raised in the original "Limits to growth" remain extremely important, and that the original limits to growth study, although subject to intense criticism, remains a fairly good predictor of actual conditions some 50 years later (Hall and Day 2009; Turner 2008; Fig. 4). Perhaps the most important issue that mankind faces is whether or not, to protect our climate and the ocean's pH, we can move away from a carbon-based global economy to one based on something else, probably wind turbines and photovoltaics. This is a systems problem in the extreme. While many prescriptions, slogans, and exhortations are offered (e.g., Jacobson et al. 2017), it is critical to assess the issue comprehensively and quantitatively, in other words with a systems approach. In my mind, no one can address this problem without reading and considering very carefully the excellent quantitative analyses of Capellan Perez et al. (2019), King and van den Bergh (2018) and Dupont et al. (2020) (and in a very different way Friedemann 2016 and Ahmed 2017). These papers are outstanding examples of how a systems approach can be and must be used to address very complex issues, and are possibly the best modern manifestations of the limits to growth. They do not predict gloom and doom, nor give technological cornucopian solutions, but help us understand what we need to know if we are to indeed generate a sustainable society. Given the fact that many trillions of dollars of investments hinge on understanding these issues well and the thin state of our quantitative analysis of the issues of energy futures, it is astonishing to see the degree to which our Universities and Governments are NOT supporting efforts commensurate with the problem, which may be existential for civilization.

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