

PERSPECTIVES

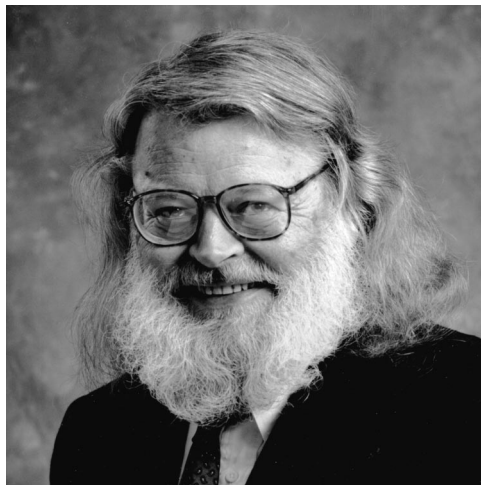
THE ROBERT H. MACARTHUR AWARD LECTURE

Ecology, 82(12), 2001, pp. 3275–3284
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IS IT TIME TO BURY THE ECOSYSTEM CONCEPT? (WITH FULL MILITARY HONORS, OF COURSE!)¹

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ROBERT V. O'NEILL, MacArthur Award Recipient, 1999

Abstract. The ecosystem concept has become a standard paradigm for studying ecological systems. Underlying the ecosystem concept is a “machine analogy” derived from Systems Analysis. This analogy is difficult to reconcile with our current understanding of ecological systems as metastable adaptive systems that may operate far from equilibrium. This paper discusses some logical and scientific problems associated with the ecosystem concept, and suggests a number of modifications in the paradigm to address these problems.

Key words: *ecosystem; ecosystem stability; ecosystem theory; ecotone; Homo sapiens; natural selection; system dynamics; Systems Analysis.*

INTRODUCTION

The term ecosystem was coined by Tansley in 1935. But as Botkin (1990) points out, the underlying concept goes back at least to Marsh (1864). Nature was viewed as relatively constant in the face of change and repaired itself when disrupted, returning to its previous balanced state. Clements (1905, 1916) and Elton (1930) offered plant and animal succession as basic processes that permitted relative constancy by repairing damage. Forbes (1925) described the northern lake as a micro-

cosm, a relatively closed, self-regulating system, an archetypic ecosystem.

Science emerged from the Second World War with a new paradigm, Systems Analysis (e.g., Bode 1945), which seemed uniquely suited for this “balance of nature” concept, and fit well with earlier work on the stability of interacting populations (Nicholson and Bailey 1935). Systems Analysis dealt with complex systems as interconnected components with feedback loops (Hutchinson 1948) that stabilized the system at a relatively constant equilibrium point. Systems Analysis can be seen underlying E. P. Odum’s (1953) definition of the ecosystem as a “. . . natural unit that includes living and nonliving parts interacting to pro-

Manuscript received 22 June 2000; revised 5 March 2001; accepted 6 March 2001.

¹ Presented 9 August 1999 in Spokane, Washington, USA.

duce a stable system in which the exchange of materials between the living and nonliving parts follows circular paths”

The machine analogy, inherent in Systems Analysis, became a central paradigm for many ecologists (Odum 1971, Holling 1973, Waide and Webster 1976). The paradigm offered a practical approach to the enormous complexity of natural systems (Teal 1962, Van Dyne 1969). The paradigm helped harness the power of the computer in ecosystem models (Olson 1963). The paradigm permitted a holistic view of system properties such as nutrient cycling (Webster et al. 1974). The familiarity of the machine analogy facilitated the communication of ecological concepts to the public.

If the ecosystem concept has held such a central place in ecology and been so productive of new ideas, why call it into question? The simple fact is that the ecosystem is not an a posteriori, empirical observation about nature. The ecosystem concept is a paradigm (sensu Kuhn 1962), an a priori intellectual structure, a specific way of looking at nature. The paradigm emphasizes and focuses on some properties of nature, while ignoring and de-emphasizing others. After a half century of application, the paradigm is showing some rust. Limitations in the concept are becoming more apparent and leading to a vigorous backlash toward ecosystem concepts in particular, and ecology in general.

BACKLASH AGAINST THE ECOSYSTEM CONCEPT

Part of the backlash results from the apocalyptic fervor of the environmental movement over past decades. Ecology oversold its ability to predict doom, and is now seen as unnecessarily constraining human freedom and economic growth. Influential opponents simply dismiss the prophecy (Simon 1980), and offer optimistic counterclaims (Naveson 1993). Human ingenuity is seen as sufficient to feed, clothe, and supply energy to an ever-growing population for the next seven billion years (Myers and Simon 1994)!

Clearly, there are ideological underpinnings to this backlash. Anything that limits human development is immediately suspect. Nevertheless, the critique highlights important limitations in ecological theory (Shrader-Frechette and McCoy 1993, Shrader-Frechette 1995, Callicott 1996). The critics claim that the ecosystem concept isn't a scientific theory at all, simply a statement about physical constraints on living things (Sagoff 1997). Concepts like stability and ecosystem are ambiguous and defined in contradictory ways. In fact there is no such thing as an integrated, equilibrium, homeostatic ecosystem: It is a myth (Soule and Lease 1995)!

If there is no stable equilibrium, why bother to conserve? Protecting and restoring endangered species is unnecessary, species go extinct all the time. How do you restore ecosystems when you don't know what to restore them to? Fragmentation actually increases spe-

cies diversity by adding edge species. Eutrophication leads to lakes with greater productivity. There isn't any environmental crisis at all!

It is important to recognize that not all of the backlash has an ideological bias. The ecosystem concept is also broadly criticized within ecology. One of the clearest statements is given by Pickett et al. (1992): “The classical paradigm in ecology, with its emphasis on the stable state, its suggestion of natural systems as closed and self-regulating, and its resonance with the nonscientific idea of balance of nature, can no longer serve as an adequate foundation for conservation.”

There is the temptation, of course, to respond defensively to the backlash. After all, the ecosystem theory being attacked is a sort of historical artifact, a “straw man.” Ecosystems are now seen as disequilibrium, open, hierarchical, spatially patterned, and scaled (O'Neill et al. 1982, Pickett et al. 1992, Levin 1999). Many of the criticisms have been addressed as the theory matured. But rather than provoking a defensive reaction, perhaps the backlash should motivate a careful re-examination of the ecosystem concept.

SCIENTIFIC PROBLEMS

The ecosystem concept is a paradigm, i.e., a convenient approach to organizing thought. Like any paradigm, it is a product of the human mind's limited ability to understand the complexity of the real world. In the case of ecological systems, we are faced with hundreds to thousands of interacting populations. The systems vary through time in complex ways, and they are spatially heterogeneous at every scale.

The ecosystem concept takes these impossibly complex phenomena and focuses on a small subset: the average or integrated properties of all the populations within a specified spatial area. This approach has the advantage of identifying “emergent” properties such as energy flow and nutrient cycling, and permits study of the relative stability of this abstract structure and its function.

But in order to gain these advantages, the concept accepts a set of assumptions that limits our thinking and determines the questions we ask. Therefore, we must continuously examine the assumptions, and consider the questions they might keep us from asking. Most importantly, we must examine whether the assumptions limit our ability to answer the very questions, such as relative stability, that the concept was designed to address.

The proposed exploration is rendered difficult by the ambiguity of terms like complexity, ecosystem, and stability. Pimm (1984) pointed out that a change in these definitions can lead to significantly different conclusions about stability. At present, the terms “ecosystem” and “ecosystem theory” are used in many different ways. At one extreme, ecosystem is a convenient term, relatively free of any assumptions, that indicates the interacting organisms and abiotic factors

in an area. At the other extreme, ecosystem is a precisely defined object of a predictive model or theory. As a result, any limiting assumption that is offered here may be disavowed by some subset of ecologists. Nevertheless, the critical examination is important, even if no single ecologist would admit allegiance to the total set of assumptions. With this difficulty in mind, let us consider some implicit assumptions and their impact on addressing stability.

Spatial closure

The ecosystem concept considers a specific spatial unit: classically, a small watershed for terrestrial systems and a lake for aquatic systems. The concept looks within these boundaries to locate the significant dynamics that require explanation and the significant processes that will explain the dynamics. The boundaries may be open to the exchange of organisms, energy, and matter. Nevertheless, the ecosystem concept assumes that the interactions and feedback loops necessary and sufficient to explain dynamics occur within the boundaries.

The problem with this assumption is that the spatial distributions of the component populations may be much larger than the ecosystem boundaries. Indeed, even the home ranges of individuals may be larger than the ecosystem, particularly for predators. This leads to anomalies, such as food web calculations determining that an ecosystem can support one half of a top carnivore, without specifying which end. But importantly, dispersal from outside system boundaries is a critical mechanism for system stability. Thus, an internal process, recovery, is not explicable by feedbacks occurring within the system specifications. The critical observation is that a forest plot surrounded by continuous forest behaves differently from that same forest plot in isolation. At the minimum, the spatial context of the system and all its component populations must be included in the specifications of the ecosystem. The stability properties of an ecological system cannot be explained by a paradigm that only considers dynamics occurring within the ecosystem boundaries.

Spatial homogeneity

A second assumption of the concept is spatial homogeneity. Spatial heterogeneity within the spatial unit is averaged in order to focus on integrated or emergent properties. And yet it is the internal heterogeneity, or the heterogeneity of the larger spatial context, that maintains the full range of populations needed to maintain stability. Without the heterogeneity, for example, pioneer species are not maintained, and recovery becomes impossible or follows an unpredictable course. A homogeneous ecosystem, like an overspecialized species, cannot respond to change and is inherently unstable. The critical observation is that two forest plots may have identical average properties, but different relative stability if they differ radically in spatial

heterogeneity. The stability of an ecological system cannot be predicted by a theory that ignores heterogeneity.

Latin binomials are substitutable

Most ecologists consider the species list critical to the definition of an ecosystem, often designating ecosystem types by their dominant species. Nevertheless, some degree of substitutability is implicit in the ecosystem concept. For example, an impacted ecosystem would be considered "recovered" if succession replaced the dominant species, and brought the system back to the same physiognomy and functional attributes. But the species list of soil organisms, for example, need not be identical. The functional properties of the system are restored, but with an altered species list. In fact, in much of ecosystem theory, the stated variables are functional groups, such as trophic levels, and which of several species perform the function is not considered.

The ambiguity introduced by species substitutability is often unrecognized. But the inconsistencies are brought out by the seemingly inane question: "Do ecosystems die?" Consider, for example, a northern lake that has undergone eutrophication. If the ecosystem is defined as a functional system at a spatial location, then the lake is the same ecosystem, albeit altered by changed conditions. On the other hand, if the ecosystem is defined by the species list, then the oligotrophic ecosystem has been killed and replaced by a eutrophic ecosystem. The ecosystem defined by a species list is almost always unstable because it rarely, if ever, recovers to the identical list of species.

If the ecosystem is defined by the species list, the only stable systems are found in extreme conditions with impoverished species lists, such as the Arctic tundra. In such conditions, recovery occurs to the same species list because only a few species can survive. But this leads to the anomalous conclusion that stability is inversely related to biodiversity. Although the biodiversity-stability relationship is questionable (see e.g., Huston 1994), the relationship suddenly reverses and becomes crystal clear. The probability of a system recovering to an identical species list is dependent on how long the list is, making tundra ecosystems more stable than tropical forests!

The dilemma would seem to be solved by defining the ecosystem by the rate processes plus dominant species. But problems still arise in dealing with stability. Consider a marine fouling community (Sutherland 1974) that may recover to the same rate processes, but any of several different species lists. In Serengeti-Mara woodlands, elephants and fire interact to produce a variety of stable states (Dublin et al. 1990, Dublin 1995). Are these stable ecosystems with several final states? Or are these unstable ecosystems?

The problem is compounded by evidence from the pollen record. Over glacial cycles, the record shows

that species respond individually to changing conditions (Davis 1976). Different species, even dominants, move in or out of an area based on their individual responses to temperature and other changes (Delcourt and Delcourt 1987). As a result, intact communities of organisms do not move as a unit, and the collection of interacting species at a location is continuously changing. The conservative conclusion is that the entity "ecosystem" is unstable. The more radical conclusion is that ecosystems, defined by their species list, don't exist and never have.

The solution to the problem would seem to involve ignoring the species list altogether and assuming perfect substitutability. The stable entity is the collection of functional groups that recover to the same rate processes, feedbacks, and complex organization. Indeed, this solution is the one implicitly adopted in many applications of the ecosystem concept. But this solution also leads to anomalous conclusions when applied to ecological phenomena other than stability.

Consider, for example, the phenomenon known as the ecotone. The ecotone is a tension zone where one vegetation type changes suddenly into another, e.g., grassland into scrub (Hobbs 1986) or forest (Hansen et al. 1994). These transitions have long attracted the attention of ecologists (e.g., Clements 1897, 1905, Livingstone 1903, Griggs 1914). But the ecotone is defined by a change in the species list, particularly in the dominants. Since environmental constraints are very similar on either side of the ecotone, rate processes would also be expected to be very similar. If the ecosystem is defined strictly in terms of function, there is not a different ecosystem on either side of the ecotone. In fact, the ecotone doesn't exist!

Nevertheless, if we limit consideration to stability phenomena, a functional definition with an assumption of species substitutability seems the logical choice. The abstraction and the associated assumptions limit the utility of the theory for explaining other phenomena, such as ecotones. Of course, this means that the ecosystem concept is not adequate as a general theory of ecological phenomena, but at least it permits explanation of stability. The functional theory defines an entity that maintains a trophic structure, recycles nutrients, and recovers from disturbance. Minimizing the role of latin binomials seems to permit a consistent framework for dealing with stability.

Natural selection minimized or ignored

The assumption of species substitutability minimizes the role of natural selection. This may be the concept's most serious limitation in dealing with stability. Natural selection is relegated to a background role causing component populations to optimize or maximize their share of resources. As a result, functional groups can be assumed to be operating at the rates set by physical and chemical constraints. Ecosystem dynamics can then be predicted from these constraints. Stated another

way, natural selection is assumed to operate slowly. Therefore, its dynamics can be assumed to be constant over the time scales relevant to ecosystem behavior. But the advantage gained may not outweigh the losses. Natural selection is the most powerful predictive theory available to ecology.

In the extreme, ecosystem specification may simply ignore the identity of component populations. But this extreme admits of a *reductio ad absurdum*. The forest ecosystems of eastern North America have lost the cougar, woodland bison, wolf, and bear. The presettlement Passenger Pigeon population is estimated at 3 to 5 billion (Schorger 1955). In the 1870s, Audubon estimated a single flock at 136 million. It moved "... like a tornado through the forest ..." breaking off trees up to two feet in diameter when it roosted (Schorger 1955). It is absurd to maintain that rate processes and stability were not altered by replacing these woodland species with *Homo sapiens*. In fact, many invasive species have this same disruptive property. Examples include cattle, kudzu, coconut, and zebra mussel.

The simple empirical fact is that ecosystems are collections of interacting populations. The component populations have been shaped by natural selection. The resulting biotic potential determines ecosystem dynamics just as much as chemical and physical constraints. Critically, natural selection is one of the processes that determines system stability.

Stability is a scaled concept

A different ambiguity arises because the concept of stability cannot be defined independently of the scale of observation. The dependence on scale is revealed when one considers the full spatiotemporal spectrum of disturbances. Disturbances that are frequent and smaller in spatial scale than the defined ecosystem boundaries can be counteracted by internal mechanisms. The ecosystem would be considered stable to these disturbances. Up to some point, the ecosystem also recovers from larger scale disturbance, i.e., disturbances that have greater spatial extent and occur less frequently. Recovery now involves mechanisms, such as dispersal, which are not ordinarily considered as internal ecosystem processes. Nevertheless, we could still consider the ecosystem as responding stably.

Ultimately, of course, the ecosystem is unstable. It is only a matter of time until a disturbance of sufficient intensity and spatial extent overwhelms the ecosystem's ability to respond. Examples include broad-scale desertification and rare asteroid collisions. Over a sufficiently long period of time, the cumulative probability of a catastrophic event approaches 1.0.

The problem would seem to be solved by specifying the time period of concern, e.g., the ecosystem is stable over millennia. But ambiguities remain. If stability depends on the spatial extent of disturbances, then the size of the ecosystem matters. The relative stability of two systems that differ radically in size cannot be ex-

plained by internal mechanisms. If the disturbance regime is the same, the smaller ecosystem is logically less stable because it can sustain itself over a shorter period of time. If the disturbance regime is radically different, the relative stability of similar-sized ecosystems cannot be explained by internal mechanisms. The ecosystem in the harsh environment is logically less stable because it can sustain itself over a shorter period of time. To deal with stability resulting from internal mechanisms requires that the definition of the ecosystem itself specify (1) the disturbance regime, and (2) the size of the specific system under consideration.

Another way to view the scale problem is to consider how we use the term "disturbance." Once the boundaries of the ecosystem are delimited, the continuous distribution of environmental variability is divided into internal conditions and external disturbances. Small-scale variability, such as the daily light cycle, seasonal temperature changes, or the occasional death of a dominant individual are considered to be part of ecosystem dynamics. Larger scale variability, such as wildfire, is not considered to be part of ecosystem dynamics.

By focusing on the ecosystem as a self-regulating, integrated system, we are led to focus on that system's resistance to disturbances, minimizing the impacts, and resilience or recovery from disturbance back to some optimal state or states. Disturbances are viewed as a damaging external interference. Yet it is well documented that preventing damage can be catastrophic. The obvious examples are management practices that prevent small wildfires. The spatiotemporal spectrum of environmental variability determines ecosystem stability just as surely as internal feedback mechanisms. Therefore, ecosystem stability cannot be explained unless the disturbance regime is part of the specifications of the ecosystem.

Homo sapiens is not a component of the ecosystem

The ecosystem concept typically considers human activities as external disturbances to the ecosystem. Other invasive pests, such as kudzu and brown rats, are considered as ecosystem components, and their impact on structure and function considered explicitly. *Homo sapiens* is the only important species that is considered external from its ecosystem, deriving goods and services rather than participating in ecosystem dynamics.

If there was ever a species that qualified as an invasive pest, it is *Homo sapiens*. The litany is familiar but merits repetition. Since 1850, the human population has quintupled, and per capita energy use has quadrupled (Holden 1991). Human inputs of nitrogen now exceed natural rates of nitrogen fixation (Vitousek 1994), and nitrogen saturation leads to the loss of other important nutrients, such as calcium (Vitousek et al. 1997). Inputs of nitrogen to the North Atlantic have increased by a factor of two to twenty compared to pre-industrial inputs (Howarth et al. 1996). Average tem-

perature is increasing faster than it has in the last 10 000 yr (Arrhenius and Waltz 1990). The human economy uses 40% of net primary production (Vitousek et al. 1986). Soil erosion is nearly universal, with soil losses exceeding soil formation rates by at least 10-fold (Pimentel 1993).

It is clear that *Homo sapiens* has altered the physical environment of the ecological system. We have changed process rates ranging from productivity to dispersal. We have changed ecological structure by eliminating our competitors, e.g., timber wolves, and even food species, e.g., Passenger Pigeon. It becomes facetious to talk about sustainability and continued extraction of goods and services when we cannot specify with any scientific rigor how *Homo sapiens* has already altered the stability properties of the system.

Summary

The importance of the definitional ambiguities becomes apparent if we consider the reasons for coming up with the ecosystem concept in the first place. The theory provides an explanatory framework for ecological phenomena. Without reverting to a naive concept of the balance of nature, the relative stability of ecological systems represents a fundamental phenomenon to be explained. Therefore, an adequate theory must be able to deal with stability. At present, the ambiguity involved in the definition of an ecosystem leads to basic problems in explaining stability. Therefore, the ambiguities undercut the very purpose for which the concept was devised.

The focus on internal dynamics and stability creates a mindset that excludes relevant phenomena. In fact, the most fundamental observation is sustainability under conditions of constant change. The stasis implied by the ecosystem concept is self-limiting. The critical property is the ability to change state in response to a continuous spectrum of change and variability. Sustainability of ecological systems involves two anti-theoretical elements: (1) local and short-term stability in the sense of recovery from disturbance, and (2) flexibility in the sense of maintaining variability of structure in space and time because conditions will change.

ELEMENTS OF A NEW PARADIGM

None of the criticisms offered in the previous section are new. Many would seem to be addressed by sophisticated developments in ecosystem theory involving, for example, nonlinear dynamics and fuzzy set theory. Unfortunately, the developments make the ecosystem theory more intriguing for mathematicians, but less useful and intuitive for biologists. I would offer for consideration that none of the developments address all of the ambiguities, and that we are putting splints and patches on an old horse.

What is proposed here is not a complete theory. What is offered is a set of principles that might lay the foundation for such a theory. In essence, these principles

constrain the theory to (1) be explicitly scaled, (2) include variability, (3) consider long-term sustainability in addition to local stability, and (4) include population processes as explicit system dynamics. The first step is to include the spatial context in the system definition.

1) *An ecological system is composed of a range of spatial scales, from the local system to the potential dispersal range of all of the species within the local system.*

The recovery of the local ecological system depends critically on the ability of individuals and populations to disperse into an impacted area. Dispersal is a critical ingredient in explaining the stability of ecological systems (Huffaker 1958). Therefore, the minimal area required to explain recovery is not the boundary of the local ecosystem, but the dispersal range of its component biota.

2) *The potential dispersal range is set by (a) the environmental constraints (biotic and abiotic) for each species, by (b) dispersal barriers, and by (c) species dispersal mechanisms.*

The critical area is not the total distribution of the species, but that portion of the range that is accessible to the local ecological system of interest. A dispersal barrier, e.g., human land use, may mean that the potential dispersal range is much smaller than the total distribution of the species. On the other hand, human activities may expand the potential range by providing new dispersal routes that permit the invasion of non-indigenous species.

Thus, human use of space may have critical impacts on stability by creating dispersal barriers. In constricting the potential dispersal range, society limits the total range of environmental variability to which the local ecosystem can respond stably. For example, a small dam makes the upstream ecosystem unstable to any fluctuation that kills fish and other organisms that must migrate back into the area to permit recovery. Here the scaled impact is insidious because immediately following construction of the dam, the upstream ecosystem and its internal feedback mechanisms appear intact.

Thus, *Homo sapiens* is a keystone species, like the beaver (Naiman et al. 1986) or starfish (Paine and Levin 1981), that alters the structure of its ecological system. By introducing dispersal barriers, *Homo sapiens* excludes populations even though the site is within their potential dispersal range. And by constructing invasion pathways, *Homo sapiens* introduces populations that would not otherwise occur. As a result, land use change becomes a component of stability dynamics. *Homo sapiens*, as a dynamic component of the ecological system, may have more far-reaching impacts on stability than society viewed as extracting goods and services from the local system.

3) *The potential dispersal range is not constant or uniform.*

Over time, this potential dispersal range can change, for example, with changes in climate. In addition, geo-

logic events may create or remove dispersal barriers. These changes may happen slowly and monotonically, permitting adaptive responses by component populations, or they may occur rapidly and produce cataclysmic changes. In addition, conditions within the potential dispersal range are not uniform. They vary on a large scale along environmental gradients, and they vary locally due to soils, topography, aspect, etc. Thus, the spatiotemporal variability that can be ignored within the boundaries of the local system may be critical, and must be explicitly considered before the stability of the local system can be predicted.

4) *Within the potential dispersal range is an effective dispersal range that is time-scaled to the problem at hand.*

Typically, an individual study focuses on a limited range of scales. For simplicity, consider a regularly repeating impact on a local ecological system. The interval between impacts determines an effective dispersal range, i.e., the distance over which the populations needed for recovery can move and become established before the next impact. Over geologic time, the effective dispersal range might equal the complete potential dispersal range. For smaller scales or more frequent impacts, the effective dispersal range would be much smaller.

5) *Within the local system, populations interact to maximize biotic potential.*

A local ecological system, such as a watershed, forest stand, or lake, has three factors that determine dynamics. First, the physical conditions at the site form a constraint set that determines the dynamic potential. Second, the potential biota are constrained to the populations whose distributions overlap at this site. Within these physical and biotic constraints, the populations then interact to form complex networks and feedback loops.

Competition and dominance determine what subset of the potential biota actually function on the site and may permit a variety of different states for the site. As a result, the list of species currently resident on a site is not necessarily sufficient to explain the range of potential system responses to impact. Indeed, flexibility in the species list is critical to the sustainability of ecological systems across the geologic scale of variability.

Competition operates within the constraints of physical laws, such as thermodynamics, and the interacting populations move toward maximizing the biotic potential of the site. The biotic potential forms an attractor, and interactions, such as nutrient cycling, move the set of populations toward this potential. But nutrient cycling is an emergent property that cannot be explained by competition alone. Energy flow and nutrient cycling operate on the same spatiotemporal scale as competition, and it is the combination of the two dynamics that results in ecosystem function.

6) *As the local ecological system approaches the*

biotic potential of a site, it increases local stability, but decreases global sustainability.

As the system develops feedback loops and complex networks of interactions, it becomes better adapted to local conditions and more stable to local impacts. But, over longer time scales, conditions change continuously. So as the system approaches the present attractor by maximizing biotic potential, it becomes suboptimal to the changed conditions. A process analogous to species specialization occurs.

The existence of local attractors becomes conspicuous at the ecotone. A small change in the environment changes the competitive relationship between dominants, and as disturbances destroy the existing vegetation and open the opportunity for new vegetation to take over the site, a different system of interacting populations gains a competitive advantage. The critical observation is that a small change in conditions has shifted the local attractor. The system that converged to one attractor becomes suboptimal when the attractor changes. It follows that the tendency to converge to a local attractor may also make the system vulnerable to changes in the attractor.

What maintains the sustainability of ecological systems over long periods of time is heterogeneity in time and space. Heterogeneity is not an annoyance that complicates experimental designs, it is a critical ingredient in explaining the stability of ecological systems (Roff 1974a, b). Consider, as an extreme case, that a uniform plain with no variation in time could result in the loss of pioneer and successional species required for recovery when the inevitable impact does occur.

The consideration of heterogeneity recommends an important change in ecosystem theory. The stability of the system depends on two complementary and scaled processes. Stability to smaller scale impacts depends on the system's ability to resist change and recover with resilience. But long-term stability or sustainability depends on a flexibility of response that can only be maintained in an environment that varies in time and space.

7) Stability of the local ecological system depends on the time scale of observation and the critical balance between (a) rates of change in environmental condition, and (b) rates of change in the biota.

Over short intervals of observation, environmental variability is likely to be small and the local system will appear stable. Over geologic time, the probability of a catastrophic event approaches 1.0 (Crowley and North 1988), and the local system is unstable. Even in the absence of catastrophic events, gradual change in the environment may eventually move the local system across a critical threshold, change the local attractor, and make the local system unstable. Thus, the relative stability of two systems is not simply measured by the rate of recovery from a disturbance, but also by the expected length of time until the next catastrophic event.

If rates of change in the conditions are slow, or the recurrence interval of disturbances is long relative to the rates of response by the local system, then the system is stable. If rates of change are rapid or the recurrence interval is short, relative to rates of response, the ecological system is unstable. If rates of change are nearly equal to rates of response, the system will appear to be highly variable or even chaotic (Phillips 1996). For this reason, human manipulations of the disturbance regime are just as important as disrupting the structural and functional integrity of the local system itself.

8) Stability of the local ecological system depends on the spatial scale of observation and the critical balance between (a) the size distribution of disturbances, and (b) the effective dispersal ranges of the biota.

If the spatial extent of the ecological system under consideration is large, for example, approaching the size of an ecoregion, then only extremely large and rare disturbances can overcome its ability to respond stably. If a local system of small extent is being considered, for example, an isolated forest plot, then the probability of a destabilizing event increases proportionately.

If the spatial extent of disturbances is small relative to the size of the ecological system, then spatial heterogeneity will be maintained within the effective dispersal ranges of biota, and the system will be stable. If the disturbances are large and approach the effective dispersal range of pioneer and successional species, the system will be unstable. If the disturbance size and effective dispersal ranges are nearly equal, the local system will appear highly variable or chaotic.

Clearly, time and space scales are related (O'Neill 1988). Stability depends on disturbance intervals relative to recovery rates, and the spatial extent of disturbances relative to the spatial extent of the effective dispersal range (Turner et al. 1993). The critical observation is that the internal interactions and feedback mechanisms within the local system are only one of a number of processes determining stability. The life history and dispersal ability of component populations, and the heterogeneity of the landscape must also be considered.

9) Homo sapiens is a keystone species that changes system stability by altering environmental constraints, rate processes, and biotic structures.

The impact of *Homo sapiens* is not limited to the quantity of goods and services extracted from the ecosystem. The long-term impact of this keystone species will likely be determined by the way it alters the stability properties of ecological systems.

Homo sapiens changes the frequency distribution of disturbances. For example, the suppression of small wildfires changes the competitive advantage of fire-resistant dominants and alters biotic structure (Botkin 1990, Buell et al. 1954). Fire suppression also decreases

es the small-scale heterogeneity of the landscape and increases the probability of larger fires. All of these impacts change the stability properties of the system.

By fragmenting the spatial structure of the landscape, *Homo sapiens* alters habitat connectivity and dispersal rates (Gardner et al. 1993). By creating dispersal barriers, this species decreases the potential dispersal range of endemic species. By creating dispersal pathways, this species greatly increases the effective dispersal range of exotics (D'Antonio and Vitousek 1992). Changes in landscape structure, such as habitat loss, can be particularly insidious if an extinction debt is incurred, and observable species loss does not occur until much later (Tilman et al. 1994, Loehle and Li 1996). Once again, these changes impact the stability properties of the system even though they are not direct effects on the interactions and feedback mechanisms within the local ecological system.

Homo sapiens is changing the physical and chemical constraint space within which ecological systems operate. The average changes, e.g., in mean temperature, may be small and result in minor changes in average rate processes. But even small changes can switch the local attractor and move the system to a new state. Goldemberg et al. (1996) point out that even modest increases in temperature can exclude crops that are intolerant to the additional few extreme days. Similarly, the temporal extremes of temperature at the spatial extremes of system distribution are likely to move ecotones by switching the local attractor.

The assertion that *Homo sapiens* is impacting the stability properties of ecological systems is not extreme or apocalyptic. Sackcloth and ashes are not required, just a review of documented examples that have already occurred (e.g., Loehle 1989): Extensive coral reefs have been destabilized (Hughes 1994), and grazing has destabilized semi-arid savannas (Walker et al. 1969, Loehle 1985). In the extreme, overgrazing turns the savanna to barren desert (Hills 1966). Nutrient additions have destabilized oligotrophic lake ecosystems (Recknagel 1985, Carpenter et al. 1998). Harvesting has destabilized competitive interactions leading to the extinction of many fish populations (Watt 1968, Jones and Walters 1976). Extensive agriculture destabilized large areas of the United States to drought, resulting in massive erosion and the Dust Bowl (Kahn 1995). Theoretical studies provide the explanation for such destabilization in complex ecological systems in general (May 1977), and ecosystems in particular (O'Neill et al. 1982, 1989). Tainter (1988) points to the possibility of similar mechanisms in the collapse of human societies.

The fundamental problem is that *Homo sapiens* is moving ecological systems outside the envelope of conditions that have existed over evolutionary history. This is terra incognita and the assumption that ecological systems will respond stably is unjustified.

CONCLUSIONS

Is it time to bury the ecosystem concept? Probably not. But there is certainly need for improvement before ecology loses any more credibility. This paper suggests some of the key problems. Spatial pattern, extent, and heterogeneity are critical to stability. You cannot get a predictive theory if you assume them away. Temporal variability and scale are critical to stability. You cannot get a predictive theory if you assume them away either. It is the interplay of natural selection and internal feedback mechanisms that determines dynamics. Again, you cannot get a predictive theory if you assume either away. Basically, all the processes and constraints needed to explain stability are not encompassed within the boundaries of the local ecological system.

An improved paradigm would have many implications for ecological applications, such as conservation. Increasing the size of an isolated preserve only increases the length of time until the cumulative probability of a disruption approaches 1.0. Maintaining dispersal pathways might better conserve sustainability by keeping the potential dispersal range near its original, undisturbed scale.

There are also important implications for monitoring. Current theory leads us to focus on average rates and standing crops at a location. Yet scale and variability in space and time may be more important in determining sustainability. Mean values at two locations may indicate that no significant change has occurred, but if dispersal pathways between the sites have been disrupted, one has reduced by orders of magnitude the scale of a catastrophic disturbance.

Perhaps the most important implication involves our view of human society. *Homo sapiens* is not an external disturbance, it is a keystone species within the system. In the long term, it may not be the magnitude of extracted goods and services that will determine sustainability. It may well be our disruption of ecological recovery and stability mechanisms that determines system collapse.

Certainly, we don't want to dismiss the current theory prematurely. But we must understand that the machine analogy is critically limited. In so far as the local system maximizes environmental potential, it necessarily sacrifices stability when that potential changed. The challenge to the ecological system is optimization to a moving target. Optimize too rapidly and the system is trapped in a local attractor and, like an overspecialized species, cannot adapt when conditions change. So, it would not be wise to send the old dobbie to the glue factory before we determine how well the new one takes the bit. But it certainly seems to be time to start shopping for a new colt.

ACKNOWLEDGMENTS

Oak Ridge National Laboratory is operated for the U.S. Department of Energy by UT-Battelle under contract number

DE-AC05-00OR22725. This is Environmental Sciences Division publication no. 5070.

LITERATURE CITED

- Arrhenius, E., and T. W. Waltz. 1990. The greenhouse effect: implications for economic development. Discussion Paper number 78. World Bank, Washington, D.C., USA.
- Bode, H. W. 1945. Network analysis and feedback amplifier design. Van Nostrand Reinhold, Princeton, New Jersey, USA.
- Botkin, D. 1990. Discordant harmonies. Oxford University Press, New York, New York, USA.
- Buell, M. F., H. F. Buell, and J. A. Small. 1954. Fire in the history of Mettler's woods. *Torreyia* **81**:253–255.
- Callicott, J. B. 1996. Do deconstructive ecology and socio-biology undermine Leopold's land ethic? *Environmental Ethics* **18**:369–372.
- Carpenter, S., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Issues in Ecology Number 3*. Ecological Society of America, Washington, D.C., USA.
- Clements, F. E. 1897. Peculiar zonal formations of the Great Plains. *American Naturalist* **31**:968–970.
- Clements, F. E. 1905. Research methods in ecology. University Printing, Lincoln, Nebraska, USA.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institute of Washington Publication **242**:1–512.
- Crowley, T. J., and G. R. North. 1988. Abrupt climate change and extinction events in earth history. *Science* **240**:996–1002.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics* **23**: 63–87.
- Davis, M. B. 1976. Pleistocene biogeography of temperate deciduous forests. *Geoscience and Man* **13**:13–26.
- Delcourt, P. A., and H. R. Delcourt. 1987. Long-term forest dynamics of the temperate zone. Springer-Verlag, New York, New York, USA.
- Dublin, H. T. 1995. Vegetation dynamics of the Serengeti-Mara ecosystem: the role of elephants, fire and other factors. Pages 71–90 in A. R. E. Sinclair and P. Arcese, editors. *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, Illinois, USA.
- Dublin, H. T., A. R. E. Sinclair, and J. McGlade. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* **59**: 1147–1164.
- Elton, C. 1930. *Animal ecology and evolution*. Clarendon Press, Oxford, UK.
- Forbes, S. A. 1925. The lake as a microcosm. *Illinois Natural History Survey Bulletin* **15**.
- Gardner, R. H., R. V. O'Neill, and M. G. Turner. 1993. Ecological implications of landscape fragmentation. Pages 208–226 in M. J. McDonnell and S. T. A. Pickett, editors. *Humans as components of ecosystems*. Springer-Verlag, New York, New York, USA.
- Goldemberg, J., R. Squitieri, J. Stiglitz, A. Amano, X. Shaoyong, and R. Saha. 1996. Introduction: scope of the assessment. Pages 21–51 in J. P. Bruce, H. Lee, and E. F. Haites, editors. *Climate change 1995. Volume 3: Economic and social dimensions of climate change*. Cambridge University Press, Cambridge, UK.
- Griggs, R. F. 1914. A botanical survey of the Sugar Grove region. *Ohio Biological Survey Bulletin* **1**:248–340.
- Hansen, A. J., F. di Castri, and R. J. Naiman. 1994. A new look at ecotones. *Biology International* **17**:9–46.
- Hills, E. S., editor. 1966. *Arid lands: a geographical appraisal*. Methuen, London, UK.
- Hobbs, E. R. 1986. Characterizing the boundary between California annual grassland and coastal sage scrub with differential profiles. *Vegetatio* **65**:115–126.
- Holden, J. P. 1991. Population and the energy problem. *Population and Environment* **12**:231–255.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* **4**:1–24.
- Howarth, R. W., G. Billen, D. Swaney, A. Townsend, N. Jaworski, K. Lajtha, J. A. Downing, R. Elmgren, N. Caraco, T. Jordan, F. Berendse, J. Freney, V. Kudeyarov, P. Murdoch, and Z. Zhao-liang. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. *Biogeochemistry* **35**:75–139.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* **27**:343–383.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**: 1547–1551.
- Huston, M. A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, New York, New York, USA.
- Hutchinson, G. E. 1948. Circular causal systems in ecology. *Annals of the New York Academy of Science* **50**:221–246.
- Jones, D. D., and C. J. Walters. 1976. Catastrophe theory and fisheries regulation. *Journal of the Fisheries Research Board of Canada* **33**:2829–2833.
- Kahn, J. R. 1995. *The economic approach to environmental and natural resources*. Dryden Press, Orlando, Florida, USA.
- Kuhn, T. S. 1962. *The structure of scientific revolutions*. University of Chicago Press, Chicago, Illinois, USA.
- Levin, S. A. 1999. *Fragile dominion*. Perseus Books, Reading, Massachusetts, USA.
- Livingstone, B. E. 1903. The distribution of the upland plant societies of Kent County, Michigan. *Botanical Gazette* **35**: 36–55.
- Loehle, C. 1985. Optimal stocking levels for semi-desert range: a catastrophe theory model. *Ecological Modelling* **27**:285–297.
- Loehle, C. 1989. Catastrophe theory in ecology: a critical review and an example of the butterfly catastrophe. *Ecological Modelling* **49**:125–152.
- Loehle, C., and B. Li. 1996. Habitat destruction and the extinction debt revisited. *Ecological Applications* **6**:784–789.
- Marsh, G. P. 1864. *Man and nature: physical geography as modified by human action*. Belknap Press, Cambridge, Massachusetts, USA.
- May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**:471–477.
- Myers, N., and J. Simon. 1994. *Scarcity or abundance*. Norton, New York, New York, USA.
- Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver. *Ecology* **67**:1254–1269.
- Naveson, J. 1993. Humanism for humans. *Free Inquiry Spring 1993*:24.
- Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations. *Proceedings of the Zoological Society of London* **105**:551–598.
- Odum, E. P. 1953. *Fundamentals of ecology*. W. B. Saunders, Philadelphia, Pennsylvania, USA.
- Odum, H. T. 1971. *Environment, power and society*. Wiley-Interscience, New York, New York, USA.
- Olson, J. S. 1963. Analog computer models for movement of nuclides through ecosystems. Pages 121–125 in V.

- Schultz and A. W. Klements, editors. *Radioecology*. Van Nostrand Reinhold, Cincinnati, Ohio, USA.
- O'Neill, R. V. 1988. Hierarchy theory and global change. Pages 29–45 in T. Rosswall, R. G. Woodmansee, and P. G. Risser, editors. *Spatial and temporal variability in biospheric and geospheric processes*. John Wiley & Sons, New York, New York, USA.
- O'Neill, R. V., R. H. Gardner, and D. E. Weller. 1982. Chaotic models as representations of ecological systems. *American Naturalist* **120**:259–263.
- O'Neill, R. V., A. R. Johnson, and A. W. King. 1989. A hierarchical framework for the analysis of scale. *Landscape Ecology* **3**:193–205.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* **51**:145–178.
- Phillips, J. D. 1996. Time lags and emergent stability in morphogenic/pedogenic system models. *Ecological Modelling* **78**:267–276.
- Pickett, S. T. A., V. T. Parker, and P. L. Fiedler. 1992. The new paradigm in ecology: implications for conservation above the species level. Pages 65–88 in P. L. Fiedler and Jain, editors. *Conservation biology: the theory and practice of nature conservation, preservation and management*. Chapman & Hall, New York, New York, USA.
- Pimentel, D., editor. 1993. *World soil erosion and conservation*. Cambridge University Press, Cambridge, UK.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* **307**:321–326.
- Recknagel, F. 1985. Analysis of structural stability of aquatic ecosystems as an aid for ecosystem control. *Ecological Modelling* **27**:221–234.
- Roff, D. A. 1974a. Spatial heterogeneity and the persistence of populations. *Oecologia* **15**:245–258.
- Roff, D. A. 1974b. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. *Oecologia* **15**:259–275.
- Sagoff, M. 1997. Muddle or muddle through? *College of William and Mary Law Reviews* **38**:825–993.
- Schorger, A. W. 1955. *The Passenger Pigeon*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Shrader-Frechette, K. S. 1995. Practical ecology and foundations for environmental ethics. *Journal of Philosophy* **92**:621.
- Shrader-Frechette, K. S., and E. D. McCoy. 1993. *Method in ecology*. Cambridge University Press, London, UK.
- Simon, J. 1980. Resources, population, environment: and oversupply of false bad news. *Science* **208**:1435–1436.
- Soulé, M., and G. Lease. 1995. *Reinventing nature?* Island Press, Washington, D.C., USA.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* **108**:859–873.
- Tainter, J. A. 1988. *The collapse of complex societies*. Cambridge University Press, New York, New York, USA.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* **16**:284–307.
- Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* **43**:614–624.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* **371**:65–66.
- Turner, M. G., W. H. Romme, R. H. Gardener, R. V. O'Neill, and T. K. Kratz. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecology* **8**:213–227.
- Van Dyne, G. M., editor. 1969. *The ecosystem concept in natural resource management*. Academic Press, New York, New York, USA.
- Vitousek, P. M. 1994. Beyond global warming: ecology and global change. *Ecology* **75**:1861–1876.
- Vitousek, P. M., J. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and G. D. Tilman. 1997. Human alteration of the global nitrogen cycle: causes and consequences. *Ecological Applications* **7**:737–750.
- Vitousek, P. M., P. R. Ehrlich, A. H. Erlich, and P. A. Matson. 1986. Human appropriation of the products of photosynthesis. *BioScience* **36**:368–373.
- Waide, J. B., and J. R. Webster. 1976. Engineering systems analysis: applicability to ecosystems. Pages 329–371 in B. C. Patten, editor. *Systems analysis and simulation in ecology*. Academic Press, New York, New York, USA.
- Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1969. Stability of semi-arid savanna grazing systems. *Ecology* **69**:473–498.
- Watt, K. E. F. 1968. *Ecology and resource, Management*. McGraw-Hill, New York, New York, USA.
- Webster, J. R., J. B. Waide, and B. C. Patten. 1974. Nutrient cycling and the stability of ecosystems. Pages 1–27 in F. G. Howell, J. B. Gentry, and M. H. Smith, editors. *Mineral cycling in Southeastern ecosystems*. ERDA Symposium Series, CONF-740513.