

The Ecosystem as a Multidimensional Concept: Meaning, Model, and Metaphor

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ABSTRACT

The ecosystem is a fundamental ecological concept that is not as simple as it first appears. We explore three key dimensions of the concept that make it both complex and broadly useful—its basic definition, its application via models to concrete or specific situations, and its metaphorical connotations as used in general communication within the domain of science and with the public at large. Clarity in identifying what the dimensions are and how they are related can help to maintain the rigor of

the concept for specific scientific uses while also allowing enough flexibility for its use in the integration of scientific principles, as well as in public discourse. This analysis of the ecosystem as a multidimensional concept is likely to be generalizable to other important concepts in ecology.

Key words: ecosystem concept; ecosystem definition; metaphor; model; specification; values.

INTRODUCTION

The purpose of this paper is to explore the various ways that the contemporary concept of the ecosystem can be used. Why analyze one of ecology's most familiar and widely used concepts? Because, far from being simple and straightforward, the ecosystem is in fact a subtle and complex concept. The multiple layers of its meaning and use can result in confusion, thereby limiting the utility of the concept. Furthermore, these layers of meaning and use have specific yet often unrecognized theoretical linkages. We intend to explore its complexity in a straightforward way. Several of the insights we draw on have been articulated before. However, to our knowledge, this essay is the first attempt to synthesize a full assessment of the complexity of the ecosystem concept. The analysis is timely because concepts and their use evolve through time as a

science and its application mature. Furthermore, peeling back the layers of complexity and examining the theoretical implications of the ecosystem concept may serve as a model for the analysis of other multifaceted ecological concepts. We will conclude by briefly indicating how our analysis of the ecosystem concept can serve as a paradigm for simplifying the complexity of other ecological concepts.

There are at least three linked, yet different, ways that the concept of the ecosystem can be used. Each of these uses can be considered a separate dimension of this complex concept. The three dimensions are meaning, model, and metaphor. The first dimension—meaning—is a technical definition that can be used in a wide variety of situations. However, for the definition to actually be used in a given situation, a domain and a variety of features must be specified (Jax 1998). Therefore, the second dimension is a model that embodies the specifications needed to address the many real or hypothetical situations that the definition might apply to. Fi-

nally, there is a metaphorical dimension that appears in informal scientific discussions, in common parlance, and in public dialogue (Golley 1993). Because these three uses are so disparate, and because ecologists and others use the concept without being clear about which dimension they are referring to at a given time, we set out to describe, contrast, and link the three kinds of uses.

MEANING: WHAT IS AN ECOSYSTEM?

The three dimensions of the ecosystem concept are meaning, model, and metaphor. We begin by addressing the abstract definition, or meaning, of the ecosystem. This dimension answers the question, "What is an ecosystem?" The basic definition of the ecosystem was first articulated in 1935 by Sir Arthur Tansley. Tansley's presentation is remarkable for its clarity, generality, and inclusiveness. It is also remarkable among the founding documents of ecology in still being widely read and accessible (Real and Brown 1991). Tansley defined the ecosystem as a biotic community or assemblage and its associated physical environment in a specific place. Because Tansley wanted to emphasize the links between the biotic and the abiotic components of ecosystems, he chose a term from physics—"system"—that highlighted interactions. Furthermore, he presented both the abiotic and biotic components as complexes. Therefore, the main components of the concept are its abiotic and biotic features and the interactions between them. Because the components of the ecosystem are themselves complexes within which there are interactions, a nested hierarchical structure is implied in the basic definition.

The definition has other important characteristics. First, it is scale independent (Allen and Hoekstra 1992). An ecosystem can be of any size so long as organisms, physical environment, and interactions can exist within it. Given this first characteristic, ecosystems can be as small as a patch of soil supporting plants and microbes; or as large as the entire biosphere of the Earth. However, all instances of ecosystems have an explicit spatial extent. The extent must be specified and bounded (Likens 1992; Odum 1993). Such specification is in fact the reason that the concept needs the second dimension of models.

Another important feature of the basic definition is that the ecosystem concept is free of narrow assumptions. It is not restricted to equilibrium, or complex, or stable systems. In fact, ecosystems may be far from equilibrium, so that they are changing in composition, content, or the processing of nutri-

ents and energy (Holling 1973). Similarly, ecosystems may be autotrophic or heterotrophic (Odum 1989). They may be simple, such as those that contain only a few microbes and some detritus exported from elsewhere. Likewise, they may be fleeting, remaining in existence only a short time. Of course, the Earth abounds in persistent and complex ecosystems as well (Odum 1971). In addition, ecosystems can include humans and their artifacts. Tansley (1935), in his seminal definition, was at pains to emphasize that ecologists should study ecosystems that incorporate humans and human-generated processes and structures (Odum and Odum 1976; Odum 1977; Costanza and others 1993; Christensen and others 1996; Grimm and others 2000).

The power of the general definition articulated by Tansley (1935) is that it is applicable to any case where organisms and physical processes interact in some spatial arena. Therefore, the basic definition covers an almost unimaginably broad array of instances. The use of the ecosystem as a core idea invites a wide variety of approaches, from biodiversity, through evolutionary, to nutrient and energy processing, from instantaneous to historical, and from microbial to biospheric (Jones and Lawton 1995). However, the power of the general definition can only be captured and used effectively if there is a framework or way to organize the huge array of cases and approaches. Therefore, a second dimension of the ecosystem concept is required to specify how the abstract definition is being used in a specific case or range of cases (Jax 1998). The second dimension comprises models.

MODEL: HOW ARE ECOSYSTEMS BUILT AND HOW DO THEY WORK?

Because the conceptual definition of the ecosystem is neutral in scale and constraint, models are necessary to translate the definition into usable tools (Pickett and others 1994). Translation requires that the parts, interactions, and scope of the system of interest be specified. Some of the features of ecosystem models are determined by the researcher, based on the questions guiding the research or application; whereas other features emerge from the nature of the material system under study. Models may be verbal, graphical, diagrammatic, physical, or quantitative. This section briefly expands on these ideas and gives examples of the diversity of models that are used to translate the general definition of the ecosystem into a working research tool.

Ecosystem models encompass a wide range of perspectives. Their variety reflects the paradigmatic breadth of ecology (Pickett and others 1994). Ecology arose at the intersection of organismic biology and various physical sciences (Hagen 1992; Golley 1993); it ranges from population genetics, evolution, and physiological ecology at one extreme, through landscape ecology and biogeochemistry at the other (Likens 1992). In addition, ecologists are increasingly exploring their links with the human sciences (Golley 1993; Cronon 2000), a relationship that has deep roots (Park 1936; Odum 1971; Odum 1977). It is a testament to its rigor that the concept of the ecosystem is relevant throughout this amazingly broad spectrum. Ecosystem models are applied all along this disciplinary breadth while retaining the basic structural requirement that ecosystems encompass a biotic complex, an abiotic complex, the interaction between them, and a physical space.

Types of Models

Various ecosystem models have been developed based on the diverse foci of energy, nutrients, organisms, and the inclusion of human sciences. One common focus of ecosystem models is energy. This perspective recognizes that living systems are nonequilibrium thermodynamic systems that require a flow of energy for their maintenance. How energy is processed, partitioned, and dissipated has engaged ecologists since the early days of the discipline (Golley 1993). Food web models are the most common kinds of ecosystem energetic models (Slobodkin 1960; Odum and Odum 2000). Sophistication has been added to energetic models by the recognition that systems as disparate as cities and oyster reefs require more than the immediate throughput of energy (Odum 1971). The energy needed for the concentration, acquisition, and distribution of the energy actually used in throughput has to be accounted for in ecosystem energetic models. This idea is embedded in the concept of “emergy” introduced by H. T. Odum (1994).

With roots as deep as those of energetic models, nutrient models have considered the material budgets of ecosystems, including pollutants (Bormann and Likens 1970). In addition, nutrient models incorporate the chemical and biological processes responsible for transforming nutrients from one chemical species to another, as well as transferring nutrients between biotic components (Agren and Bosatta 1996).

Another kind of ecosystem model that is gaining in importance is biodiversity modeling (Mooney

and others 1995). Foci in this area include the roles of species richness, species identity, keystone species, functional groups, and assembly rules in ecosystem processes. The aim of these models is to clarify the role of various kinds of biological diversity in ecosystem function (Schulze and Mooney 1993; Perrings and others 1994; Hooper and Vitousek 1998).

Ecologists and economists are currently working together to establish the new discipline of ecological economics (Ehrlich and Mooney 1983; Costanza 1991; Daily 1997). One of the essential tools of this discipline is a type of ecosystem model that exposes the nature and environmental role of economic instruments and economic work (Jansson and Jansson 1994; Costanza and Folke 1997; Costanza and others 2000). The countercurrent flows of money and energy and the role of economic institutions are accounted for in these models (Odum 1971; Holling 1994).

As researchers from the fields of ecology, ecological economics, and the social sciences interact more effectively, ecosystem models are beginning to incorporate the full range of human institutions that affect energy, nutrient, and economic flows (Berkes and Folke 1994; Odum 1994; Machlis and others 1997; Pickett and others 1997). In particular, models are emerging that account for human capital (individual knowledge and skills) as well as social capital (community, political, formal, and informal institutions) (Folke and others 1994; Grove and Burch 1997; Costanza and others 2000).

The ecosystem models enumerated so far concentrate on the biotic and social components and the fluxes in ecosystems. Explicit focus on the physical space occupied by the ecosystem helps to refine ecosystem models by examining the role of the physical template (Holling 1973). The physical template may include physical and biological components, and the heterogeneity of this ecosystem template may have functional significance (Pickett and others 2000). Natural and human disturbances and ecological engineers are central features of models incorporating the ecosystem template (Jones and others 1994). The feedback between the physical template and the biotic or human components of the ecosystem has emerged as an important functional linkage in this type of model (Christensen and others 1996; Dale and others 2000).

Despite their variety, these ecosystem models—perhaps surprisingly—share some key features. First, the conceptual definition of the ecosystem is expressed in all of these disparate models. Each one

includes some sort of biotic complex, an abiotic complex, and the interactions that connect the complexes internally and with each other; finally, each model takes place in an identified or implied spatial area. Moreover, the models specify the nature of these complexes, locations, and the included interactions. They do so by possessing a domain that is determined in part by the research question and in part by the biological and physical constraints imposed by the research question.

Domain of Model

The following steps are needed to establish the domain of a model: (a) identify the components of the model, (b) state the spatial and temporal scale addressed by the model, (c) delimit the physical boundaries of the system, (e) articulate the connections among the components, and (f) identify the constraints on system behavior (Odum 1993; Pickett and others 1994). The components of the models are the biological, social, or geophysical entities that are of interest—for example, species, populations, soils, patches, nutrients, energy, and various kinds of capital. The model identifies the components that will be included and specifies at what level of aggregation they are evaluated (Jax and others 1998). For example, organisms can be considered as individuals or as communities.

The second step in establishing the domain of a model is to state the spatial and temporal scale and the resolution it employs (Allen and Hoekstra 1992; Odum and Odum 2000). Temporally, ecosystem models can have seasonal, decadal, or even longer extents. Spatially, ecosystem models can range from fine to coarse scales. For example, a watershed model can incorporate large catchments or focus within a watershed on patches that produce or capture runoff.

Because ecosystems are conceived as spatial units, their boundaries must be specified (Likens 1992). Boundaries allow ecologists to simplify their systems so that models can be tractable, to identify an external set of forcing functions, and to precisely calculate and follow changes in material and energy budgets (Odum 1993). The boundaries of an ecosystem can be set for many reasons including (a) as a matter of convenience, (b) to follow geomorphological divides, (c) to understand a political entity, (d) to recognize changes in flux rates, or (e) to respond to changes in the frequency of some ecological process of interest. Convenience and physical borders are the most common motivations for setting ecosystem boundaries.

The domain of a model must also make the connections in the system explicit. Exactly what components and entities are linked to one another? Which ones are only indirectly connected? What parts of a system are tightly coupled and which only weakly coupled? Is there a hierarchical structure of functional components in a system based on the strength of coupling? These questions are among those that must be addressed when describing how the components of an ecosystem model are connected.

The connections merely indicate which components are linked. How they are linked is exposed by identifying the intervening ecological interactions and influences. The kinds of interactions that are included in the model depend on the type of model being built. Processes can be transfers and alterations of the form of energy and matter, transfers of capital, or behavioral, genetic, or informational influences.

A model domain must also identify the constraints on system behavior. Depending on the processes and components included in the model, various principles will be relevant to the model and may constrain the behavior of system components. For example, cybernetic theory suggests that persistent ecosystems will contain negative feedback loops; thus, attention needs to be paid to the role of feedback loops in general in ecosystem models (Odum 1988). Another example of an assumption derived from the physical sciences arises from thermodynamics, which suggests that energy throughput will play a role in the self-organization of ecosystems (Morowitz 1968). For example, in nutrient-based models, the principles of conservation of matter and stoichiometry are crucial constraints (Agren and Bosatta 1996). Nutrient models that focus on the processing of nitrogen in riparian zones, for example, are informed by the physiology of nitrification and denitrification, in which the availability of oxygen acts as a critical switch. Models of water dynamics in ecosystems may combine the hydrological concept of the “variable source area” with generalizations from the physiology of whole-plant water use. Models of the role of changing biodiversity in ecosystems will be constrained by knowing the limits to evolutionary diversification.

The domain articulated by the researcher is affected by the choice of an equilibrium or nonequilibrium approach to the model dynamics (Holling 1973). An equilibrium model assumes that ecosystem behavior is governed by a single stable domain of attraction (Golley 1993). Thus, succession tends toward a single fixed climax, or perturbation of

nutrient cycles ends in recovery of the predisturbance flux and allocation among pools. In this approach, numerical constancy and deviation from a quantitative reference is emphasized. In contrast, nonequilibrium ecosystem models emphasize the degree of persistence of systems (Holling 1986). Qualitative states of the system, dynamic fluctuations, and pulses of resources or regulators are dominant features of nonequilibrium ecosystem models. Nonequilibrium models may exhibit multiple domains of attraction, shifting stable states, spatially dynamic mosaics, and system resilience. Dynamic ecosystem models focusing on resilience appear to be especially appropriate for human ecosystems and the assessment of sustainability (Holling 1994).

Use of Models

The richness of topics, complexity of model domains, and range of behaviors that models can exhibit suggest that ecosystem models can be used for diverse purposes. One obvious use of ecosystem models is in the quantification of energy and material budgets. For example, the rigor of watershed nutrient budgets has led to important insights about ecosystem restoration, succession, and sensitivity to continental-scale atmospheric deposition of pollutants (Likens and others 1996; Vitousek and others 1997). Applying this rigor to human-dominated ecosystems may help to promote projects related to restoration and sustainable design (Westley 1995).

Models can also be useful to facilitate communication among scientists. Within a discipline, models clarify the assumptions and structures that individual scientists or groups deem to be influential in a system of interest. When models are used for interdisciplinary research, they reveal which of those assumptions and structures are shared by those disciplines and which are contradictory (Pickett and others 1999). Thus, interscientist communication can result in new models, appropriate cross-disciplinary assumptions, and clarity in terminology and parameters.

Clarity within and between disciplines permits models to generate testable alternatives. Ecosystem models are based on principles drawn from physical, chemical, organismal, evolutionary, and spatial sciences. A thorough assessment of the principles from these various disciplines that may be relevant to the behavior of an ecological system can help to identify which are necessary to provide the fundamental structure of the model, which act as switches or controllers, and which are not relevant to the dynamics at hand (Shachak and Jones 1995). Ecologists must also determine which principles have not yet been

proven to be significant to the behavior of the model. Finally, they must decide whether the equilibrium or the nonequilibrium approach will be more successful in portraying the behavior of a particular system. In other words, principles that may represent sound science outside the sphere of ecosystem ecology can be extrapolated to serve as testable hypotheses or tentative assumptions in ecosystem models.

Finally, models provide a useful means of communication with the public and decision makers. Stakeholders interested in the use or outcome of an ecosystem model can be instrumental in the actual construction of the model (Costanza and Folke 1997). Involving stakeholders through a process of mediated modeling can help to ensure that relevant and respected models are built. There are convenient tools available, such as STELLA, that both the public and scientists can use in mediated modeling (Hannon and Ruth 1994). Ultimately, when the models are up and running, they can provide the entire spectrum of the public—from individuals and households, to institutions and agencies, to managers and decision makers—with technical information about the behavior of the human ecosystems they inhabit or manage. This use of models leads us to consider the final dimension of the ecosystem idea—the ecosystem as metaphor.

METAPHOR: WHAT ARE ECOSYSTEMS LIKE AND WHY ARE THEY VALUABLE?

The two dimensions of the ecosystem discussed so far are both in the technical realm and therefore require precision and accuracy for their use. However, the ecosystem also has an informal and symbolic use in more general parlance. In its metaphorical sense, the ecosystem represents one or more other concepts or values (Golley 1993; Ulanowicz 1997). Structural metaphors for the ecosystem as a whole include the ecosystem as a machine, the ecosystem as an organism, and the ecosystem as an algorithm. Behavioral metaphors include ecosystems as resilient structures or ecosystems as fragile structures (Cronon 1995).

Metaphors can be used in two kinds of situations—scientific and social. In science, metaphor plays a generative or creative role (Pickett 1999). A process under investigation, especially in its early development, may be likened to some other phenomenon. For example, in evolution, artificial selection or plant and animal breeding served as a metaphor for a core mechanism of evolutionary change, natural selection (Young 1985). An exam-

ple in ecology can be found in the early development of the theory of succession. Successional changes in vegetation were likened to the development of an organism when it was first codified theoretically (Clements 1916). Although vegetation development is in no sense the same thing as the growth, maturation, and senescence of an individual organism, the metaphor helped Clements (1916) and others extract some useful generalizations that organized the study of a multifaceted process. The fact that succession can proceed in many different ways and from a multitude of causes (Glenn-Lewin and van der Maarel 1992) could be understood once simple expectations had emerged from metaphorical images of development. Metaphors and the more general phenomenon of analogies are crucial stimuli to synthesis and innovation (Pickett and others 1999).

Metaphors for scientific concepts are also common in public discourse (Holling 1986; Golley 1993). This arena of communication includes education, the media, policy making, and management. In such public uses, the precision and narrow focus of technical terms is eschewed in favor of richness of connotation and in support of societally important, if sometimes controversial, values. Rather than attempt a comprehensive roster, we will give only a few examples. These examples illustrate two kinds of metaphorical uses—reference to place and reference to attributes.

The ecosystem is often used as a metaphorical representation of some place on the Earth's surface. This type of use has its roots in Tansley's (1935) technical definition, a key component of which is place (Golley 1993). Examples include such uses as "the marsh ecosystem." This is a powerful use because it focuses attention on specific kinds of places and the generalizations about them. In addition, such metaphorical use can focus on specific sites, as in "the Gwynns Falls Park ecosystem." This more specific spatial metaphor is powerful because it invokes a sense of responsibility and empowerment.

The ecosystem as place, although useful, is a rather shallow metaphor in the public discourse. However, in fact, people do often associate values with ecosystems as place (Callicott 1992; Christensen and others 1996). Values are moral or ethical stances taken by people, groups, or institutions. For example, public use of "the ecosystem" can stand for a plethora of attributes people appreciate—or alternatively, detest—in the natural world (Cronon 1995). Therefore, values can be connoted metaphorically by the term "ecosystem." Connectedness is one such attribute. "Everything is con-

nected to everything else" can be either a comforting or a threatening metaphorical description of the ecosystem, depending on one's perspective. Such an idea can express people's value of kinship with nature, or their cautionary approach to natural resources. Values can also be exploited in teaching people about ecosystem processes. If one recognizes that an audience values connectedness, that idea can be used to teach people that ecosystems include feedbacks in general or lagged and indirect effects in particular.

In addition, the concept of the ecosystem can be used to stand for equilibrium, resistance or resilience, diversity, and adaptability. Some of these connotations are only hypothetical from the perspective of science, whereas others are clearly unsupported or highly problematical (Wu and Loucks 1995). The point here is not to evaluate the veracity of such connotations, but only to point to their richness and power in the public discourse (Norton 1992). Although precision is valued in the technical use of the ecosystem concept, one of the major benefits of its use in public discourse arises from its ability to reflect a wide array of processes, values, and kinds of interactions. A wide variety of stakeholders can be brought together by its flexibility because all of them will find some connection with their individual concerns (Costanza and Folke 1997).

Using the ecosystem concept in public discussions, which extend from the deliberations of courts of law, to administrative regulation, institutional decision making, and individual behaviors, adds important dimensions to those discussions. Moreover, its use can alert scientists to the public concerns and interests represented by the ecosystem concept (Rozzi 1999) and serve as an entry point for ecologists to inject more scientific knowledge and greater clarity into the public discourse. However, the values and assumptions attached to the concept in public dialogue may sometimes create hostility toward the introduction of scientific information. Therefore, it is important for scientists who want to engage in public discussions of important environmental issues to understand the values connoted by public use of the ecosystem concept.

The metaphorical uses discussed thus far have dealt with ecosystems as a whole. But metaphors can also be used to apply to parts of ecosystem models or their outputs. One such metaphor is the ecological footprint (Rees 1992), which stimulates ecologists to extend the spatial boundaries of urban ecosystems to incorporate outlying areas that supply resources and process wastes. A similar meta-

Table 1. Metaphorical Origins of Four Technical Terms in Ecology

Competition 1. The act of seeking or endeavoring to gain that for which another is also striving; rivalry; strife for superiority; as in the competition of two candidates for office. From Latin, <i>competetre</i> , to strive together.
Evolution 1. The act of unfolding or unrolling; a process of development, formation, or growth. From Latin, <i>evolutio (-onis)</i> , an unrolling or opening; <i>e-</i> , out, and <i>volvere</i> , to roll.
Landscape 1. A picture representing a section of natural, inland scenery, as of pasture, woodland, mountains, etc. From Dutch, <i>land</i> , land, and <i>schap</i> , ship.
Succession 1. The act of succeeding or coming after another in order or sequence or to an office, estate, etc. From Old French, thence Latin, <i>successio (-onis)</i> , a coming into the place of another.

From Webster's Universal Unabridged Dictionary, 2nd ed. 1983. New York: Dorset & Baker.

phor is a life support area (Jansson and Jansson 1994). The metaphor of ecosystem services (Daily 1997) helps to convert the outputs of ecosystem models into socially valuable terms. The metaphor of natural capital (Folke and others 1994; Perrings 1994) recognizes that biological and biologically mediated resources are limited within ecosystems. All of these metaphors help to engage new researchers in modeling or investigating ecosystem processes and functions, as well as helping the public to understand ecosystem behavior and value (Costanza and others 2000).

FLEXIBILITY OF THE ECOSYSTEM CONCEPT

The ecosystem concept has proven to be immensely flexible and productive (Golley 1993; Jax 1998). There are several realms in which its flexibility is readily apparent. Within science, the ecosystem has supported budgetary approaches (Odum and Odum 2000), studies of individual processes (Agren and Bosatta 1996), and studies of the reciprocal interactions between disparate organisms and their effects in particular sites (Holling 1995). It can be an analytic or a synthetic concept (Golley 1993), and it can support an impressive variety of kinds of models (Ulanowicz 1997). Ecosystem science, starting from the basic definition of Tansley (1935), has expanded to include many kinds of studies (Likens 1992; Jones and Lawton 1995; Pickett and others 1997).

The concept now supports studies that incorporate humans not only as externally located, negative drivers (Odum 1971) but also as integral agents that affect and are reciprocally affected by the other components of ecosystems (Jansson 1984; McDonnell and Pickett 1993; Costanza and others 2000). Studies of urban ecological systems have shown clear evidence of its flexibility (Grove and Burch 1997; Pickett and others 2001). Moreover, it has even proved useful in ambitious at-

tempts to understand system change and institute policies of adaptive management (Holling 1995; Westley 1995).

In addition, the ecosystem concept has promoted the synthesis of ideas in ecology. Studies of populations, communities, and the various influences that structure them have often been pursued independently of each other, as well as independently of studies of biogeochemistry. But in recent years, studies that integrate aspects of population, community, and biogeochemistry have become increasingly more common (Jones and Lawton 1995). This expansion of ecosystem science is entirely consistent with the scope and breadth of the ideas first formulated by Tansley in 1935.

A PARADIGM FOR ECOLOGICAL CONCEPTS

As we have shown, the ecosystem concept has three dimensions. One is its basic technical definition, which is remarkably free of limiting assumptions concerning equilibration, closure, stability and persistence, components, and kinds of interaction. Second is its need and ability to be specified through a variety of kinds of models that articulate components, interactions, extent and boundaries, fluxes, system structure, and permitted dynamics. Finally, its metaphorical use stimulates synthesis and integration within the domain of science and can also carry a variety of socially significant assumptions.

The ecosystem concept is not alone in its multidimensionality. It is likely that all important and widely significant ecological concepts have these same three dimensions—a core definition that is neutral in scale and constraint, the capacity and need to be specified in different cases through various kinds of models, and a metaphoric aspect that stimulates both scientists and the public (Pickett and others 1994). Competition, succession, evolution, and landscape are examples of

other concepts that are multidimensional. These four examples are especially telling because they existed first in their metaphorical and social uses (Table 1). When they were applied in science, their technical definition and use in models required isolation from the metaphorical dimension. Therefore, in a mature science, the metaphorical assumptions must be stripped from the core definition, while scale, process, content, bounds, fluxes, currencies, and dynamics must be specified in particular models. The metaphorical dimension allows science to be injected into the public discourse, but it also introduces the problem of “unpacking” the baggage of often contradictory assumptions and values that are a necessary part of social and political discourse (Rozzi 1999). Researchers can make better use of these core concepts and terms by first recognizing their multidimensional nature.

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REFERENCES

- Ågren G, Bosatta E. 1996. *Theoretical ecosystem ecology: understanding element cycles*. New York: Cambridge University Press.
- Allen TFH, Hoekstra TW. 1992. *Towards a unified ecology*. New York: Columbia University Press.
- Berkes F, Folke C. 1994. Investing in cultural capital for sustainable use of natural capital. In: Jansson A, Hammer M, Folke C, Costanza R, editors. *Investing in natural capital: the ecological economics approach to sustainability*. Washington (DC): Island Press. p 128–49.
- Bormann FH, Likens GE. 1970. The nutrient cycles of an ecosystem. *Sci Am* 223:92–101.
- Callicott JB. 1992. Aldo Leopold’s metaphor. In: Costanza R, Norton BG, Haskell BD, editors. *Ecosystem health: new goals for environmental management*. Washington (DC): Island Press. p 42–56.
- Christensen NL, Bartuska AM, Brown JH, Carpenter S, D’Antonio C, Francis R, Franklin JF, MacMahon JA, Noss RF, Parsons DJ, and others. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. *Ecol Appl* 6:665–91.
- Clements FE. 1916. *Plant succession: an analysis of the development of vegetation*. Washington (DC): Carnegie Institution of Washington.
- Costanza R, editor. 1991. *Ecological economics: the science and management of sustainability*. New York: Columbia University Press.
- Costanza R, Daly H, Folke C, Hawkin P, Holling CS, McMichael AJ, Pimentel D, Rapport D. 2000. Managing our environment portfolio. *BioScience* 50:149–55.
- Costanza R, Folke C. 1997. Valuing ecosystem services with efficiency, fairness, and sustainability as goals. In: Daily GC, editor. *Nature’s services: societal dependence on natural ecosystems*. Washington (DC): Island Press. p 49–68.
- Costanza R, Wainger L, Folke C, Mäler K-G. 1993. Modeling complex economic systems: toward an evolutionary, dynamic understanding of people and nature. *BioScience* 43:545–55.
- Cronon W. 2000. Resisting monoliths and tabulae rasae. *Ecol Appl* 10:673–5.
- Cronon W, editor. 1995. *Uncommon ground: toward reinventing nature*. New York: Norton.
- Daily GC. 1997. Introduction: what are ecosystem services? In: Daily GC, editor. *Nature’s services: societal dependence on natural ecosystems*. Washington (DC): Island Press. p 1–10.
- Dale VH, Brown S, Haeuber RA, Hobbs NT, Huntly N, Naiman RJ, Riebsame WE, Turner MG, Valone TJ. 2000. Ecological principles and guidelines for managing the use of land. *Ecol Appl* 10:639–70.
- Ehrlich R, Mooney HA. 1983. Extinction, substitution, and ecosystem services. *BioScience* 33:248–54.
- Folke C, Hammer M, Costanza R, Jansson A. 1994. Investing in natural capital—why, what and how? In: Jansson A, Hammer M, Folke C, Costanza R, editors. *Investing in natural capital: the ecological economics approach to sustainability*. Washington (DC): Island Press. p 1–20.
- Glenn-Lewin DC, van der Maarel E. 1992. Patterns and processes of vegetation dynamics. In: Glenn-Lewin DC, Peet RK, Veblen TT, editors. *Plant succession: theory and prediction*. New York: Chapman & Hall. p 11–59.
- Golley FB. 1993. A history of the ecosystem concept in ecology: more than the sum of the parts. New Haven: Yale University Press.
- Grimm NB, Grove JM, Pickett STA, Redman CL. 2000. Integrated approaches to long-term studies of urban ecological systems. *BioScience* 50:571–84.
- Grove JM, Burch WR Jr. 1997. A social ecology approach and application of urban ecosystem and landscape analyses: a case study of Baltimore, Maryland. *Urban Ecosys* 1:259–75.
- Hagen JB. 1992. *An entangled bank: the origins of ecosystem ecology*. New Brunswick (NJ): Rutgers University Press.
- Hannon B, Ruth M. 1994. *Dynamic modeling*. New York: Springer-Verlag.
- Holling CS. 1994. New science and new investments for a sustainable biosphere. In: Jansson A, Hammer M, Folke C, Costanza R, editors. *Investing in natural capital: the ecological economics approach to sustainability*. Washington (DC): Island Press. p 447–502.

- Holling CS. 1973. Resilience and stability of ecological systems. *Ann Rev Ecol Syst* 4:1–23.
- Holling CS. 1986. The resilience of terrestrial ecosystems: local surprise and global change. In: Clark WC, Munn RE, editors. *Sustainable development of the biosphere*. New York: Cambridge University Press. p 292–317.
- Holling CS. 1995. What barriers? What bridges? In: Gunderson LH, Holling CS, Light SS, editors. *Barriers and bridges to the renewal of ecosystems and institutions*. New York: Columbia University Press. p 3–34.
- Hooper DU, Vitousek PM. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecol Monogr* 68:121–49.
- Jansson A. 1984. Integration of economy and ecology: an outlook for the eighties. Stockholm: Sundt Offset.
- Jansson A, Jansson B-O. 1994. Ecosystem properties as a basis for sustainability. In: Jansson A, Hammer M, Folke C, Costanza R, editors. *Investing in natural capital: the ecological economics approach to sustainability*. Washington (DC): Island Press. p 74–91.
- Jax K. 1998. Holocoen and ecosystem: On the origin and historical consequences of two concepts. *J Hist Biol* 31:113–42.
- Jax K, Jones C, Pickett STA. 1998. The self-identity of ecological units. *Oikos* 82:253–64.
- Jones CG, Lawton JH, editors. 1995. *Linking species and ecosystems*. New York: Chapman & Hall.
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–86.
- Likens GE. 1992. Excellence in ecology, 3: the ecosystem approach: its use and abuse. Oldendorf/Luhe (Germany): Ecology Institute.
- Likens GE, Driscoll CT, Buso DC. 1996. Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science* 272:244–6.
- McDonnell MJ, Pickett STA, editors. 1993. *Humans as components of ecosystems: the ecology of subtle human effects and populated areas*. New York: Springer-Verlag.
- Machlis GE, Force JE, Burch WR Jr. 1997. The human ecosystem part I: the human ecosystem as an organizing concept in ecosystem management. *Soc Nat Res* 10:347–67.
- Mooney HA, Lubchenco J, Dirzo R, Sala OE, Cushman JH, Janetos AC, Ehrlich PR, Templeton AR, Chapin FS III, Reynolds HL, and others. 1995. Biodiversity and ecosystem functioning: basic principles. In: Heywood VH, editor. *Global biodiversity assessment*. Cambridge: Cambridge University Press. p 311–8.
- Morowitz HJ. 1968. Energy flow in biology: biological organization as a problem in thermal physics. New York: Academic Press.
- Norton BJ. 1992. A new paradigm for environmental management. In: Costanza R, Norton BG, Haskel BD, editors. *Ecosystem health: new goals for environmental management*. Washington (DC): Island Press. p 23–41.
- Odum EP. 1993. *Ecology and our endangered life support systems*. 2nd ed. Sunderland (MA): Sinauer Associates.
- Odum EP. 1977. The emergence of ecology as a new integrative discipline. *Science* 195:1289–93.
- Odum EP. 1989. *Our endangered life support system*. Sunderland (MA): Sinauer Associates.
- Odum HT. 1994. The emergy of natural capital. In: Jansson A, Hammer M, Folke C, Costanza R, editors. *Investing in natural capital: the ecological economics approach to sustainability*. Washington (DC): Island Press. p 200–14.
- Odum HT. 1971. *Environment, power, and society*. New York: Wiley.
- Odum HT. 1988. Self-organization, transformity, and information. *Science* 242:1132–9.
- Odum HT, Odum E. 1976. *Energy basis for man and nature*. New York: McGraw-Hill.
- Odum HT, Odum EC. 2000. *Modeling for all scales: an introduction to system simulation*. San Diego (CA): Academic Press.
- Park RE. 1936. Human ecology. *Am J Sociol* 42:1–15.
- Perrings C. 1994. Biotic diversity, sustainable development, and natural capital. In: Jansson A, Hammer M, Folke C, Costanza R, editors. *Investing in natural capital: the ecological economics approach to sustainability*. Washington (DC): Island Press. p 92–112.
- Perrings CA, Mäler KG, Folke C, Holling CS, Jansson BO. 1994. Biodiversity and economic development: the policy problem. In: Perrings CA, Mäler KG, Folke C, Holling CS, Jansson BO, editors. *Biodiversity conservation: problems and policies*. London: Kluwer Academic Publishers. p 3–21.
- Pickett STA. 1999. The culture of synthesis: habits of mind in novel ecological integration. *Oikos* 87:479–87.
- Pickett STA, Burch WR Jr, Foresman TW, Grove JM, Rowntree R. 1997. A conceptual framework for the study of human ecosystems. *Urban Ecosys* 1:185–99.
- Pickett STA, Burch WR Jr, Grove JM. 1999. Interdisciplinary research: maintaining the constructive impulse in a culture of criticism. *Ecosystems* 2:302–7.
- Pickett STA, Cadenasso ML, Grove JM, Nilon CH, Pouyat RV, Zipperer WC, Costanza R. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Ann Rev Ecol Syst* 32:127–57.
- Pickett STA, Cadenasso ML, Jones CG. 2000. Generation of heterogeneity by organisms: creation, maintenance, and transformation. In: Hutchings M, John L, Stewart A, editors. *Ecological consequences of habitat heterogeneity*. New York: Blackwell, p 33–52.
- Pickett STA, Kolasa J, Jones CG. 1994. *Ecological understanding: the nature of theory and the theory of nature*. San Diego (CA): Academic Press.
- Real LA, Brown JH, editors. 1991. *Foundations of ecology: classic papers with commentaries*. Chicago: University of Chicago Press.
- Rees WE. 1992. Ecological footprints and appropriated carrying capacity: what urban economics leaves out. *Environ and Urbaniz* 4:121–9.
- Rozzi R. 1999. The reciprocal links between evolutionary-ecological sciences and environmental ethics. *BioScience* 49:911–21.
- Schulze E-D, Mooney HA, editors. 1993. *Biodiversity and ecosystem function*. New York: Springer-Verlag.
- Shachak M, Jones CG. 1995. Ecological flow chains and ecological systems: concepts for linking species and ecosystem perspectives. In: Jones CG, Lawton JH, editors. *Linking species and ecosystems*. New York: Chapman & Hall. p 280–94.
- Slobodkin LB. 1960. Ecological energy relationships at the population level. *Am Nat* 94:213–36.

- Tansley AG. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:284–307.
- Ulanowicz RE. 1997. *Ecology, the ascendent perspective*. New York: Columbia University Press.
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol Appl* 7:737–50.
- Westley F. 1995. Governing design: the management of social systems and ecosystems management. In: Gunderson LH, Holling CS, Light SS, editors. *Barriers and bridges to the renewal of ecosystems and institutions*. New York: Columbia University Press. p 391–427.
- Wu J, Loucks OL. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q Rev Biol* 70: 439–66.
- Young RM. 1985. *Darwin's metaphor: nature's place in Victorian culture*. New York: Cambridge University Press.