



The Ecosystem Concept and Linking Models of Physical-Chemical Processes to Ecological Responses: Introduction and Annotated Bibliography

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PURPOSE: The U.S. Army Corps of Engineers (USACE) is striving to design, evaluate, and manage its large-scale engineering projects in a sustainable, environmental context that extends beyond traditional project boundaries. This approach, which frames a project as part of a larger, functioning ecosystem, was articulated in “The Environmental Operating Principles” by the Chief of Engineers (Flowers 2002) and has been adopted by the System-Wide Water Resources Program (SWWRP). The goal is to promote environmental sustainability and sound stewardship by adopting an ecosystem view.

BACKGROUND: Traditionally, the design, operation, and maintenance of USACE projects have relied heavily on models (both physical and numeric) as engineering tools. The reliance on models by the USACE will continue and probably increase, but the broad view expressed in the Environmental Operating Principles requires that the capabilities of these engineering models be expanded to address more of the biological aspects of the environment (i.e., higher trophic levels and the entire ecosystem). This can be accomplished by (1) incorporating additional, ecological (biological) features into existing physical-chemical, engineering models, (2) coupling existing physical-chemical models with existing ecological models, or (3) creating entirely new models that encapsulate the necessary physical, chemical, and biological features. Because a very large investment has been made in engineering models and ecological models (both within and beyond the USACE), it is hoped that the existing inventory of models can be used to produce new modeling capabilities, without a large investment in additional models.

If ecological models are to be successfully coupled to engineering models, or if more ecological processes are to be incorporated into existing engineering models, then it is critical to understand the basic obstacles that must be overcome, and some of the fundamental, underlying principles of ecology, ecosystems, and ecological modeling. The objectives of this document, therefore, are to (1) present some of the significant concepts and obstacles that must be addressed when ecological models, which have a biological or organismal emphasis, are linked to engineering models of physical-chemical processes, and (2) provide an introduction to the ecosystem concept and its history by way of a literature review and bibliography.

MODELS AND ECOSYSTEMS: The natural world can be complex beyond comprehension, and models (mental as well as numeric) are a way to simplify this complexity. Good models only address those aspects of the system that cannot be ignored, and these models may allow for the exploration of systems and processes that cannot be directly accessed or manipulated (Heemskerk et al. 2003, Jackson et al. 2000). Models can be more or less quantitative, deterministic and mechanistic, abstract and empirical. They help define questions and concepts more

precisely, generate hypotheses, assist in testing these hypotheses, and generate predictions (Turner et al. 2001). The builder of a model must choose those aspects of the system that will be included, the frame of reference for the model, the relations of interest (or importance) between the model parts, and the mechanisms by which the parts interact. The model-building process identifies errors in assumptions and missing information; it explores the model's behavior, and reveals gaps in understanding about connections and causalities in the system. The building process can sometimes be more informative than the model itself (Levins 1966, Jackson et al. 2000, Taylor 2000).

Ecosystems. Ecosystems seem exceptionally well-suited to a modeling approach. They are complex, and their dynamic network of positive and negative interactions has parallels in the feedback and control mechanisms of systems engineering. Consequently, a linkage emerged early on between systems engineering and ecology. This merger led to the development of fields called variously "ecological engineering," "ecosystems modeling," and "systems ecology" (White et al. 1992). Rapid advances in computing capability have accelerated development in these fields, and many of the mechanistic, ecological models that have been produced are similar in many ways to the engineering models used in hydraulics and hydrology. It may seem strange, therefore, that engineering models of the physical and chemical processes associated with water and its movement are not readily coupled to models that focus on ecological patterns and processes in these same systems.

The USACE has successfully used numeric and physical models to simulate the movement of water across wide scales of time and space, ranging from seconds to years in time and centimeters to tens or hundreds of kilometers in spatial extent. Some engineering models have, in fact, combined ecological phenomena with physical and chemical processes (turbidity, nutrient absorption/desorption). But these ecological phenomena have generally been limited to those that are mediated by microorganisms (e.g. oxygen consumption, denitrification, and algal blooms), and little progress has been made in integrating ecological models of higher trophic levels (e.g. migratory fish). Such higher-level models are used extensively by biologists and are now needed increasingly by engineers involved in water resource management and restoration. Nestler et al. (2000) suggest that differing scales of interest create a fundamental difference between engineering models and most ecological-biological models, and that this difference has resulted in the development of very different modeling approaches by the two disciplines. The authors contend that these two disciplines can be successfully bridged under favorable circumstances, but it is generally far more difficult than it may at first appear; basic principles of scale and hierarchy appear to be a major source of this difficulty.

Concepts and Software Code. Not all the ecological models in wide use today are numerical simulations, some are simple quantitative, or qualitative rules, or indices, to predict biological response to the ambient environment (defined in many differing ways). Many of today's ecological models are also taking advantage of recent technological developments in geographic information systems (GIS) to expand or refine their applicability, and make them easier to use, but few, if any, are directly coupled to detailed, numeric simulations that focus on the ambient physical-chemical environment.

This document does not address the technical details of authoring computer codes that transfer data from one computer program (model) to another. This transfer of information seems

relatively straightforward and mechanical once conceptual issues are resolved and the information that can (or should) be transferred has been identified. However, the conceptual issues of how (if) information generated by one model can be made meaningful to another model operating in a totally different context of time, space, and relations seem problematic. This is the key to successful connections among models. These conceptual issues are not likely to be resolved in a generic, automatic manner that is applicable to a wide range of models and readily amenable to computer coding (i.e. expressed as a computer algorithm). Computerized “expert systems” or artificial intelligence may have the potential to facilitate the model-linking process, but this seems a rather distant possibility.

DRIVERS AND RESPONSES: Models and modelers often use the term “drivers,” which can be defined as human and biophysical forces that produce change in the biophysical patterns and processes of an ecosystem. For example, physical-chemical conditions and processes can be viewed as the primary drivers of many ecological responses. In ecological modeling, a major challenge is to appropriately link the ecological effect (or response) to its physical-chemical and biological drivers (causes). Successful numeric models have been constructed to simulate some of the important drivers in ecosystems. For example, extremely complex and successful numerical models have been created to simulate the movement of water (hydrologic and hydraulic models) across a wide range of environmental settings (from pipes to small streams to large rivers and lakes to entire oceans). The interactions of wind, water, heat, and some chemical reactions have also been successfully incorporated into these numerical models. If the issues of scale and hierarchy can be successfully addressed, then these models should be able to provide important driver information to “higher level” ecological models.

Unfortunately, many physical-chemical models are intended to explore the behavior of physical and chemical processes (such as water velocity and temperature changes) in response to changes in their own drivers or boundary conditions (e.g., the operation of a discharge structure, or precipitation), and often operate at fine scales of time and space (seconds–centimeters). They are not intended generally to provide driver input to biological-ecological processes that respond at higher levels in the hierarchy, often at coarser scales of time and space (days–kilometers) than the engineering model. In general, many existing physical-chemical models do not lend themselves directly to simulating larger-scale patterns of habitat (e.g., seasonal water velocity regimes), or biotic-abiotic interactions (e.g., light penetration and algal standing crop), or biological adaptations (at the physiological, species, or community level) that play such a large role in the biotic characteristics of an ecosystem. In particular, most of these models do not allow higher levels in the hierarchy to provide feedback that can influence events back down at their level. For example, a detailed sediment-resuspension, light-availability model is unlikely to account for longer-term changes in the environment (e.g., growth of aquatic plants) that will alter the model’s boundary conditions or basic assumptions (e.g. sediment properties or shear forces). Likewise, most typical ecological models will simplify, assume, or ignore many of the fine-scale details of the physical-chemical environment. Unless the interaction of the biota with the physical-chemical drivers is an immediate focus of an ecological model, there is apt to be no provision for the ecological model to receive input from a detailed simulation of these lower-level physical processes, nor is there apt to be any mechanism for the higher levels in the ecological model to influence (provide feedback to) the lower level processes. In most cases, the lower level processes are considered independent “drivers” of the system and the “typical” behavior of these drivers is assumed or implied, and incorporated into the various calibration factors of the ecological model.

Because the drivers are not an explicit feature in the model, any significant change in their behavior requires the model to be empirically “recalibrated.”

REFERENCE FRAMES AND CURRENCIES: In spatially explicit models that address movement and transport of objects or material, there are generally two frames of reference that can be used. One of these, named for Leonhard Euler (Swiss mathematician, 1707-1783) is the view of a system in motion from the perspective of a stationary observer. The Eulerian view tracks the motion of materials or particles through a stationary grid. The alternative approach, named for Joseph-Louis Lagrange (1736-1813) is the view of a system in motion from the perspective of an observer who is moving along with the system. The Lagrangian view tracks the properties of the particle or material as it moves. For example, in a river system, the Eulerian frame of reference is the view of the water from a stationary point on the riverbank. The Lagrangian frame of reference is the view of a water parcel as might be seen from a boat drifting along in the river current.

Most engineering models use a Eulerian framework to divide the physical domain into a grid of discrete, interconnected cells. These Eulerian models typically employ a series of assumptions (from Nestler et al. 2000):

- Processes of interest can be averaged within cells without significant loss of accuracy.
- Particles and processes are uniformly dispersed within cells.
- Individual particles lose their separate identities within cells.
- A grid-specific origin is used to implement conservation of mass and momentum concepts.
- Space within the physical domain of interest represented by the grid is organized into three-dimensional (3-D) Cartesian representation using x, y, and z axes.

The Eulerian framework appears to work best when the process being simulated integrates over small spatial scales and short temporal scales relative to the grid size and time-step so that the error produced by successive averaging processes within and between cells is small. These processes and the constituents they produce and transform can then be advected, dispersed, and transformed within the grid representation of the physical domain (Nestler et al. 2005).

By comparison, many biological or ecological models focus on individual members of higher trophic levels (such as individual fish) and in these models, the movement of the individuals, their orientation in space, and their individual histories over time are important features that must be preserved (simulated and tracked). This is more typical of a Lagrangian reference frame and the assumptions of a Eulerian framework, listed previously, are often violated by the individuals in these models (after Nestler et al. 2000), as follows:

- Individuals cannot be averaged within cells because the movement of individuals cuts across multiple/differing cells within one time-step and because their range of movement in a single time-step significantly exceeds water velocities associated with advection and dispersion. Therefore, their movement cannot be simulated using only advection and dispersion algorithms.

- If individuals are uniformly dispersed within cells and lose their individual identity, then there is substantial loss of accuracy. The movements of individuals may change with gender, size, age, stage, physiological condition, and recent history as well as ambient conditions in the surrounding environment. Therefore, the identities and histories of individuals must be preserved as they move through the model domain.
- The grid-specific global origin and vector depiction of flow fields common to Eulerian frameworks (necessary to implement conservation of mass and momentum) are inadequate to describe the spatial orientation of most large, mobile organisms. Such organisms can orient to streamlines and other features in their immediate environment and they thus use a local origin, perhaps their own location, or an immediate feature and not the global origin of a Eulerian system.

Nestler et al. (2000, 2005) have shown that in specific, well-conditioned situations, it is possible to link a Eulerian engineering model to a Lagrangian ecological model of fish movements. Therefore, these differing frameworks are not, of necessity, an insurmountable obstacle to model linkage. More details from the Nestler et al. (2005) example are presented later.

Closely related to the frame of reference used by a model is the manner in which material, energy, or information is expressed and transferred among model components, also known as model 'currency.' A major task in the development of some models is to express all exchanges and material balances in a common currency (e.g., grams of carbon). This can be awkward, artificial, and inaccurate within a single model, especially when it involves conversions between matter and energy, or between total mass and numbers of individuals, but a common currency can simplify model construction and operation. When two models are linked, it is usually necessary for the points of linkage to use the same currency. In some cases this can be a simple conversion of units (e.g. from English to metric), but in other instances, the difference may be more fundamental and conceptual, and no strict conversion is really possible (e.g. turbidity vs. suspended solids). The serious issue of currency mismatch is hinted at by Nestler et al. (2005) in their discussion of mass versus individuals in Eulerian and Lagrangian frameworks, and we can easily conceive of a difficult situation that makes simple linkage impossible. For example, suppose an ecological model is based on individuals as the response (individual fish) and also uses individuals as a driver (i.e., the concentration of algal cells per mL in a discrete vertical layer), but the candidate engineering model provides information only on total algal biomass (as grams of carbon) in two broad vertical zones. Experts who are familiar with the two models and the specific system being simulated could possibly work out an interface algorithm that would allow these two models to meaningfully communicate with each other, but it would not be a generic, automatic solution. Additional field data would probably be needed, and the accuracy of the resulting linked pair might be less than acceptable.

SCALE AND HIERARCHY: The terms scale and hierarchy have been used without much explanation to this point; a more complete introduction is now in order. Ecosystems can be viewed as organized into differing hierarchical levels that function at differing temporal and spatial scales. Each higher level in the hierarchy is comprised of the lower, simpler levels, as well as all the processes at those lower levels. In addition, the hierarchy includes a suite of interactions of a given level with the higher levels above and the lower levels beneath. For example, the dynamics of a population of salmon can be considered as one component in a higher level

aquatic community. The community level will incorporate interactions between differing populations (components at the lower level) that are not completely depicted at the level of the individual components (e.g. the salmon population). As a result, the description (and behavior) of population dynamics at the community level will likely differ from population dynamics at the population level, because additional processes must be included as hierarchical levels increase. Odum (1971) stated it simply, “An ecosystem is more than the sum of its parts.”

The concepts of scale and hierarchy in ecological systems and systems in general have been discussed at length for more than 20 years by a host of authors, including Tim Allen at the University of Wisconsin (cf. Allen and Starr 1982, O’Neill et al. 1986, Ahl and Allen 1996, Rosswall et al. 1988, Allen and Hoekstra 1992, Schneider 1994, Peterson and Parker 1998). All this activity is driven, in part, by a recognition that the processes within ecological systems operate at multiple scales of space and time and with hierarchical patterns of organization. Some ecologists have suggested that “the problem” of scale is the central question in ecology (Allen and Starr 1982, Levin 1992). The problem is how to relate processes that occur on differing scales of space and time to ecological patterns and dynamic behaviors observed on other scales of space and time, in other words, linking drivers and responses across spatial-temporal scales (King 1991, Ehleringer and Field 1993).

In the case of mechanistic physical-chemical models, the phenomena of interest, and the aspects of the system that must be included, dictate the model’s scale of time and space. These typically range from seconds to hours and from centimeters to kilometers. Because organisms and populations may integrate the effects of the environment over larger scales of time and space, many ecological models have larger time and space scales that range from days to centuries and centimeters to hundreds or thousands of kilometers, respectively. An immediate problem thus arises in connecting models with differing spatial and temporal extent. There is also a question of “grain” or resolution in these scales, and the hierarchical structures of an ecosystem (i.e. features and processes that occur at specific scales of time and space) have proven extremely troublesome in creating model linkages (numeric or conceptual).

It is important to recognize that the basic perception of ecosystem properties, such as stability (Turner et al. 2000) or predator-prey relations, is influenced by the scale of the observations. This is shown by Carpenter and Kitchell (1987) in a study of the correlation structure among ecosystem model components at differing temporal scales. When they only used observations taken every third day, they found that predator-prey effects resulted in algal production being negatively correlated with zooplankton biomass. If, however, they used observations taken every sixth day, the relation was reversed. At this scale, the levels of prey and predator are both dominated by the seasonal dynamics of nutrients, and algal production is positively correlated with zooplankton biomass. The over-arching constraint of general trophic condition, not immediately obvious at the daily scale, is the dominant factor at the weekly scale. The relation explored by Carpenter and Kitchell can be compared with the transfer of cargo back and forth from one boat to another. The immediate effect of the transfer is to cause one boat to sit lower in the water while the other rises (a negative relation). However, on a larger scale, the two boats rise and fall together on the tide (a positive relation). A model of an individual boat that focuses on the position of the deck relative to the water surface is unlikely to include the tidal rise and fall, as this larger-scale process does not seem relevant.

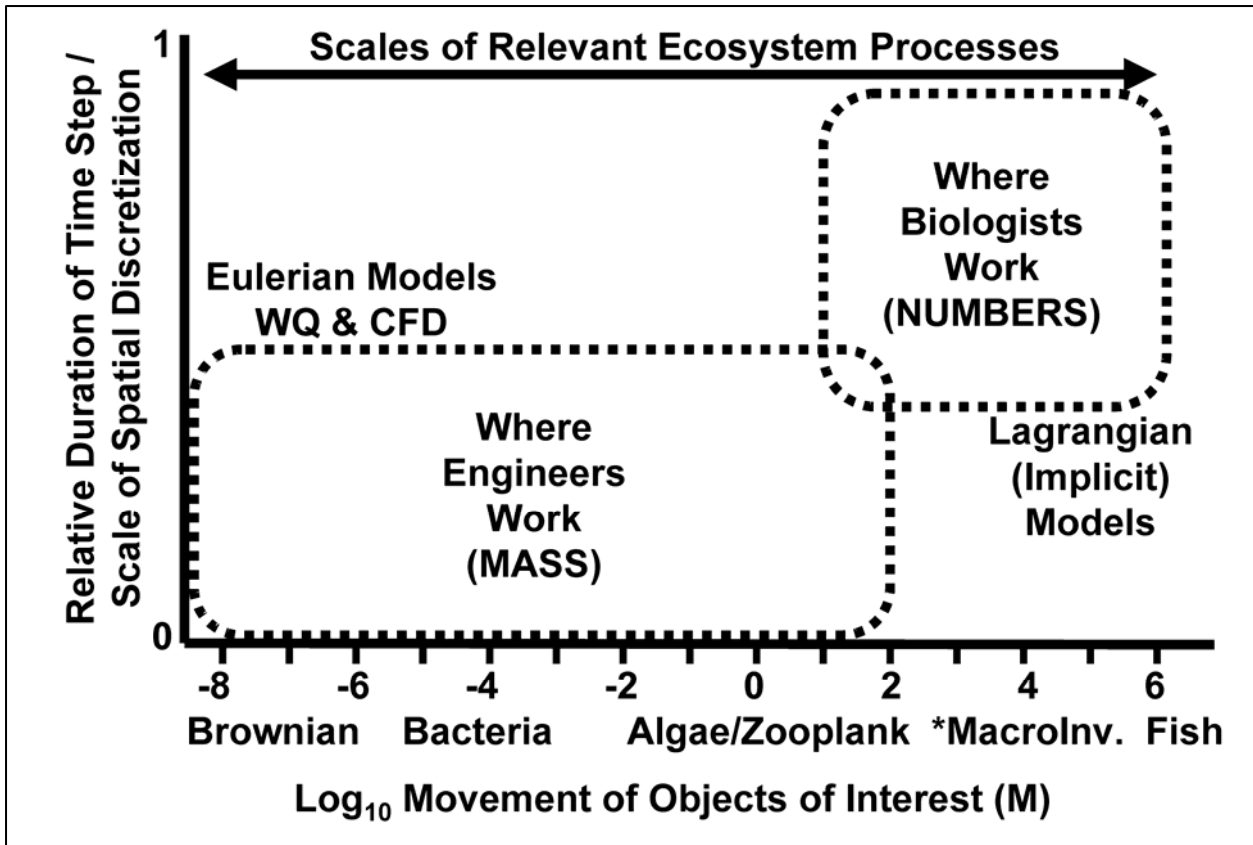


Figure 1. Scale can be a surrogate for hierarchical levels since a particular hierarchical level can be associated with a temporal and spatial scale. A comprehensive description of an ecosystem must include processes that span wide ranges in scale (Figure 1 in Nestler et al. (2000))

Natural disturbance is another example. If disturbances are large and rapid compared to the system of interest, then the ecosystem appears unstable. However, the exact same disturbances may have no such effect on the system when a larger scale is considered. For example, trees in an individual forest plot may come and go, so the status of individual trees is unstable, but if a larger scale is considered (i.e., the whole forest) then the total forest cover in the region may stay relatively constant (Vande Castle 1998) despite (or even because of) the instability in small local plots. Consequently, the fundamental nature of interconnections among model components (and the applicable scale of the model itself) is forced to reflect the scale(s) of observations that were used to develop the model.

O'Neill and King (1998) give another example from studies of net primary production. At continental scales, the spatial distribution of primary production is dominated by climate, whereas temperature and moisture determine short-term production dynamics. However, within a region where temperature and evapotranspiration are relatively homogeneous, production is dominated by slope aspect and soils (Thorhallsdottir 1991). O'Neill and King (1998) use this relation to argue that scale considerations can reconcile two ecosystem approaches discussed later: (1) Clements' (1916) continental view of plant communities constrained by climate and (2) Gleason's (1926) study of individual plant communities, where competition is the dominant driver.

From the preceding discussion it should be clear that scale and hierarchy have important ramifications for the building and coupling of ecosystem models. Scaling errors will occur if information derived from a lower level of the hierarchy is used directly (coupled) to make predictions at a higher level of hierarchy unless the interactions between components at the intervening levels are also incorporated. For example, a model of leaf photosynthesis scaled directly to the whole ecosystem without including canopy structure, rooting, nutrient availability, and other higher level constraints will probably not function correctly. Scaling up from the leaf model to the forest will require substantial, additional modeling and research or data collection.

Allen (1982) points out that ecological models that explicitly express many processes and structures at differing hierarchical levels (and are therefore composed of numerous coupled processes and interactions), tend to be complex and highly sensitive to slight changes in parameters. Suggesting a way out of this problem, Allen and Starr (1982) and O'Neill et al. (1986) find that it is seldom necessary to look more than one level down to find a mechanistic explanation of a system's behavior (e.g. biochemistry level for leaf and leaf fluxes for canopy level) and it is possible to use this concept to construct mechanistically rich ecosystem models in a hierarchical manner that remain stable and easy to manage. With this approach, they argue, the mechanistic modeling of each hierarchical layer is emphasized using the mechanisms that occur at the level directly below, coupled by constraints from the level above (O'Neill and King 1988). A given layer N in the model is parameterized by data (results) of the model at layer N-1 and constrained by the status of layer N+1.

The authors believe this suggestion points to a central impediment to coupling many mechanistic physical-chemical models to their ecological counterparts. Specifically, the ecological models contain several layers of hierarchy (explicit or implicit) that are not matched to those of the chemical-physical model, and further, the two models may be separated from one another by more than a single layer of hierarchical organization. Hence, to make a linkage between two models, it may be necessary to unravel the multiple layers of hierarchy in each of the models and create a whole new model (with all the necessary interconnections) for the intervening level(s) that separate the two model types. In many cases, this can be a daunting task and the required ecological knowledge may not exist, even if other resources are available. Further, the lower hierarchical levels represented by the detailed physical-chemical model may be mostly irrelevant (or unnecessary) to building a sound ecological model that functions at several hierarchical levels above. In any event, the process of model coupling does not seem to be one that will lend itself readily to automation, except when the candidate models are extremely well-conditioned for joining.

EXAMPLES OF MODEL LINKAGES:

Chesapeake Bay. A recent workshop (U.S. Environmental Protection Agency (USEPA) 2005) explored the coupling of a detailed, spatially explicit model of water quality (Chesapeake Bay Program Water Quality Model, CBPWQM) to a non-spatial trophic response network model (EwE, Ecopath with Ecosim) that predicts the abundance of fish species. The issues and obstacles that surfaced in the workshop provide excellent illustrations of the principles enumerated above. Those wishing to link ecological models of aquatic systems with models of the physical-chemical drivers are most strongly urged to examine the associated report (USEPA 2005). The participants noted that

One impediment to developing integrated analyses of water quality and fisheries management arises from the differences in how scientists working in these two disciplines view key processes and interactions. Water quality researchers and modelers maintain a view that ecosystem dynamics are dominated by physiological and biogeochemical processes and their associated kinetic and mass-balance relationships. Fisheries scientists, however, tend to view fish population dynamics as being dominated by organism life cycles and behaviors that are constrained by fishing mortality.

In this example, the fisheries model is clearly operating at several hierarchical layers of organization above that of the physical-chemical driver model. The “higher level” constraints experienced by the water quality model (e.g. zooplankton grazers) are several steps down the food chain from the “drivers” in the fish model. The workshop participants recognized the difficulty this created (although without reference to hierarchy theory) and proposed a commonly used approach to spanning hierarchical levels, namely the use of empirical regression equations to create “calibration” factors. Of course, the equations that result would not be the same as those obtained with “real” data, but the concept would be the same. The workshop participants also recognized that they were dealing with issues of time and space scales, mainly because the resolution (grain) of the water quality model was so much finer than that of the fish model. The attempt to couple these two modeling systems continues and is having some success, but is not a trivial undertaking and major conceptual hurdles must still be surmounted.

Peoria Lake (Illinois River). In this example from Best et al. (2004), aquatic vegetation growth models (Best and Boyd 2001, 2003) were coupled to a hydrodynamic (RMA2) and sediment resuspension (SED2D) model that helped define the light-climate (drivers) that the vegetation experienced during growth. Light limitation on growth largely determined whether the vegetation would persist, or gradually disappear. In this situation, the hydrodynamic and resuspension models were all at (or one step below) the temporal scale of the vegetation model (i.e., daily time-step) and it was relatively straightforward to feed the daily median values of water depth, current velocity, and light extinction coefficient generated by the hydrodynamic and sediment models into the vegetation growth model as input. However, this example illustrates another serious hurdle to making such linkages. It is well-known that the growth of vegetation can strongly dampen the resuspension of sediment. Thus vegetation beds play a significant role in creating their own light climate. In the coupling of these two models in this example, there is no mechanism for the vegetation to influence (provide feedback to) the hydrodynamic and resuspension models as its abundance changes. Hence, this is a unidirectional, loose coupling of these two models. This is the simplest type of interconnection between two models and it was successful for the restricted purposes of this application. In a longer-term simulation, or one that had a differing purpose (e.g., modeling the long-term light climate in the system), feedback from the vegetation to the physical-chemical environment would have been critical and substantially more difficult to incorporate.

Richard B. Russell Lake (Savannah River). In this example from a USACE reservoir, Nestler et al. (2000, 2005) explored the coupling of a Eulerian model of the physical-chemical environment (CE-QUAL-W2) with a Lagrangian model of biota (individual fish) moving through the physical-chemical environment created by the engineering model. An important

difference between this example and the more problematic Chesapeake Bay case, described earlier, was that this example does not involve multiple trophic levels of biota.

The Richard B. Russell situation seems especially well-conditioned to linkage between the two candidate models because the drivers (temperature and oxygen) provided by the engineering model are the direct cause of the modeled fish response (horizontal and vertical movement) and there is no feedback from the fish to the physical-chemical environment. In the Richard B. Russell (RBR) scenario, the primary structural feature of the environment is the reservoir's thermocline, a relatively large, uniform, and slowly changing feature (relative to the size and movement of the fish) that, from the standpoint of the fish model, can be adequately and realistically represented by a two-dimensional model.

The importance of scale becomes immediately obvious in this coupling. If the model pair is intended to show the general vertical and horizontal distribution of fish in the reservoir on a horizontal scale of kilometers, a vertical scale of meters, and temporal scale of hours or days, then the environment presented by CE-QUAL-W2 is well-suited to the need. If, however, one was attempting to model the movements of an individual fish in its immediate environment on a scale of centimeters and seconds (such as in pursuit of individual prey or a habitat microzone), then the broad, average environment provided by CE-QUAL-W2 might be less than useful. In such a case, a very high-resolution, 3-D engineering model might still provide an adequate representation of the physical environment to which the model fish would accurately respond. The nature of the candidate models and the form and function of the coupling must be customized to the questions (and scales) being addressed.

INTRODUCTION TO THE ECOSYSTEM CONCEPT: The ecosystem concept, by incorporating physical, chemical, and biological aspects of a functioning system into an integral unit, is a useful way to address complex systems and to approach resource management problems. Models of ecosystems draw extensively on the ideas of feedback and control from systems engineering, and are, to a large extent, the translation of the ecosystem concept into an interconnected collection of numeric algorithms or equations. Therefore, it is important for those who wish to understand ecosystem models, and the possible linkages among models, to have at least a brief exposure to the history, development, and literature of the ecosystem concept. A recent commentary by Pickett and Cadenasso (2002) provides one such introduction.

The many variants of the ecosystem concept that have emerged over the past century have some common features, and it is among those common features (summarized below) that a practical definition exists:

1. The ecosystem has both biotic and abiotic components.
2. These components interact in a manner that produces structure in the resulting system.
3. The interactions (processes) involve material flow or cycling as a result of energy transfer.
4. The spatial and temporal boundaries, while somewhat arbitrary, are defined in terms of interaction strengths within and without the system.

The ecosystem is the basic unit in ecology. The ecosystem is "...the basic unit of nature on the face of the earth" (Tansley 1935). These statements are taken for granted by many ecologists, but

other authors sometimes contradict these statements by identifying communities, individual organisms, or cells as the basic units of ecology. This conflict has never been fully resolved.

Whittaker (1975) defined the ecosystem as “a community and its environment treated together as a functional system of complementary relationships, and transfer and circulation of energy and matter....” Some scientists employ only the first portion of this definition, “a community and its environment.”

Worster (1977) in his excellent book on the origins of the field of ecology, described the ecosystem “as a model of interrelatedness in nature” and presenting “both the biological and non-biological aspects of the environment as one entity, with strong emphasis on measuring the cycling of nutrients and the flow of energy in the system – whether it be a pond, a forest, or the earth as a whole.”

By 1983, E.P. Odum (1983) had arrived at a definition of the ecosystem as “any unit (a biosystem) that includes all the organisms that function together (the biotic community) in a given area interacting with the physical environment so that a flow of energy leads to clearly defined biotic structures and cycling of materials between living and nonliving parts....”

However, in the original definition (Tansley 1935), the ecosystem was conceived as more of an arbitrary system to provide an alternative to the more tangible plant community prevalent in the field of ecology at that time. Specifically, Tansley wrote:

...The more fundamental conception is, as it seems to me, the whole system (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome – the habitat factors in the widest sense. Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system. It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth.

Tansley continued with,

These ecosystems, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom.

The reader should note here that there has been some discussion among historians that Tansley’s colleague, Arthur Roy Clapham, actually suggested this term to Tansley in 1930 but did not publish the idea.

Today ecosystems are studied neither at the level of the universe nor the atom. Tansley’s definition nevertheless offered great latitude for ecosystem boundaries, both in time and space. Clearly, later usage of the term ecosystem was a refinement of the original. Shugart (1990), moreover, noted that the flexibility of the meaning of the term has also been employed by systems scientists in their references to “systems of definition” or “systems of interest,” but Shugart

offered no further clarification. The strength of the concept may lie as much in its flexibility as in its structure.

Online resources on this topic can be found at these sites and many others:

- <http://www.biologie.uni-hamburg.de/b-online/e54/54a.htm>
- <http://www.al.umces.edu/currie/defofeco.htm>

Early history of ideas contributing to the ecosystem concept. The early history of the ecosystem concept has been discussed in many books and articles. In addition to Worster (1977), McIntosh (1985) presented a comprehensive background to the general field of ecology, but did not introduce the ecosystem concept until nearly halfway through his book. Both of these books are excellent, in part because the individuals who wrote them have formed coherent stories in which to present the history. A smaller book by O'Neill et al. (1986) addresses the narrower concept of hierarchy in ecosystems and also gives a concise and useful history of the development of the ecosystem concept. Golley (1993) wrote an interesting account of the history of the ecosystem concept from his personal view and experience.

Lastly, while there are many general ecology texts that summarize the history of the concept, there are also several volumes of edited collections including the classic collection by Kormondy (1965) which present, as reprints, some of the papers that are listed individually in subsequent sections of this technical note and by Real and Brown (1991).

Development of the ecosystem concept. Not surprisingly, the ecosystem concept, like so many other ideas, existed long before a term was coined to describe it.

Nowhere can one see more clearly illustrated what may be called the sensibility of such an organic complex, expressed by the fact that whatever affects any species belonging to it, must have its influence of some sort upon the whole assemblage. He will thus be made to see the impossibility of studying completely any form out of relation to the other forms; the necessity for taking a comprehensive survey of the whole as a condition to a satisfactory understanding of any part.
Forbes (1887)

Forbes' landmark paper, "The Lake as a Microcosm," thus opened with a statement essentially of the ecosystem concept nearly 50 years before the term was coined by Tansley (1935), but 10 years after a paper by Mobius (1877) in which a similar idea was termed a 'biocoenosis.' The idea that later became the 'ecosystem concept' was, by that time, obvious to anyone who understood Darwin's theory of evolution. Anker (2002) provides some additional perspective on the thoughts and motives in Tansley's mind when he coined the term, "ecosystem."

And while Darwin's (1859) theory assisted in the genesis of the ecosystem concept, it also contained the foundation for the most serious intellectual challenge to the concept. This was recognized early in the 20th century but articulated best by Harper (1977), 90 years after the Forbes paper. Harper's challenge was dependent on the fundamental assumption, articulated best by Dobzhansky (1973) that "nothing in biology has meaning except in light of evolution." This linkage between the field of biology and evolution remains solid today. But as Harper noted:

*It is an intriguing problem to examine the ecological triangle from the point of view of the evolutionist because ultimately all the discoveries of descriptive, production or population ecology must find their meaning in evolutionary phenomena. Since the time of Fisher (1930) it has become clear that evolution happens because (a) some individuals leave more descendants than others, and (b) some of the differences between individuals are heritable and affect the chance of leaving descendants. Evolutionary thinking concentrates attention on the behavior of the individual and his descendants. If nothing in biology has meaning except in light of evolution and if evolution is about individuals and their descendants – i.e. fitness – we should not expect to reach any depth of understanding from studies that are based at the level of the super-individual, whether it be the flora and fauna of the descriptive ecologist or the efficiency of production and resource cycling studies by the production ecologist or the gross population phenomena of the population biologist. **What we see as the organised behavior of systems is the result of the fate of individuals.** (emphasis added)*

This was a potentially devastating criticism of the ecosystem approach – to limit its meaning to a superficial collection of individual activities. The conflict had its roots in plant ecology early in the 20th century. And plant ecology has its roots much earlier.

One of the earliest papers that has been cited in plant ecology literature provides a description of plant succession (King 1685). The paper describes the development of peat bogs and wetlands in Ireland. In as much as this process is successional, it can be interpreted as a paper on ecological succession. But plant ecology remained largely descriptive until the 19th century and the publication of Darwin's theory. Eugenius Warming, a Danish botanist, published a book in 1895 titled, "Plantesamfund" in which he described ecology as "the manifold and complex relations subsisting between the plants and animals that form one community." His book was subsequently translated and published in English (1909). And Cowles (1899, 1901, 1911) is often cited as providing the foundation for what would become a robust inquiry into plant community development and succession.

Several persons assumed prominence during the early 20th century and they and their students were a strong influence on the field of ecology. Frederic E. Clements promoted the idea that certain communities of plants could be considered 'superorganisms' and this idea became almost dogma in ecology. One of the later works on this subject, "Plant Succession and Indicators" (Clements 1928) summarized much of the earlier research by Clements and numerous other investigators, research that led to and supported the concept of 'succession to climax' and the 'superorganism concept.' Clements, his students, and his followers formed one view of plant ecology in the early 20th century that became known as 'Clementsian' ecology.

In brief, the 'superorganism concept' supported the idea that certain tightly associated plant communities were uniquely identifiable and that they develop in a series of changes similar to evolutionary or organismal development. That is, they progress predictably through succession to a well-defined climax (adult?) community that is stable and recognizable. The feature of this idea that is relevant to the ecosystem concept is that the unit of interest includes a tightly interactive assemblage of populations, capable of displaying characteristics as a community that transcend the mere sum of the individual populations. This property is sometimes termed an 'emergent

property' or a property of a complex system that is not predictable from the behaviors of the individual components. The subtitle of Golley's (1993) book, 'More than the sum of the parts,' implies the continued presence of the superorganism concept in the ecosystem concept today.

The other major view of plant ecology at the time was one formulated by Henry Allan Gleason and became known as 'Gleasonian' ecology. Gleason's view was opposed to the 'Clementsian' view; Gleason referred to it as the 'individualistic concept of ecology' (Gleason 1917, 1926, 1939).

In Gleason's view, communities were potentially unique and their content was determined by the nearly random chance that different species of plants would be propagated to a particular habitat. This view approximated a 'null hypothesis' in which communities exist in a continuum of many potential and changing states that are dependent on individualistic activities of individual species.

The conflict between Gleason and Clements was very strong and the 'Clementsian' view prevailed for much of the early 20th century. However, as experimentation and careful observation critically tested both views, the 'Gleasonian' view came to prominence and the 'superorganism' has become less prominent, although the superorganism concept is often implied in ecosystem-level research and understanding.

Modern development of the ecosystem concept. Although plant ecologists formed much of the foundation for the ecosystem concept, a separate but not independent line of thought developed in animal ecology. The early development also dates to Darwin or before, but the systematics of Linnaeus, combined with the biological observations of Haeckel (who coined the term, 'ecology' in 1866) and others led zoologists in a progression of ideas. Mathematical or physical biology was forming a new line of thought, one that was expressed in the language of physical science. The early work by Lotka (1925) outlined mathematical representations of population growth and interaction parameters. The beauty of these numerical relationships was that relatively simple models (exponential growth, for example) could be manipulated mathematically, and the biological populations and their characteristics could be represented through the logical symbols of mathematics. For example the symbols, beginning with 'n' (the number of individuals in the population), 'r' (the intrinsic rate of growth), and 'k' (the asymptote or carrying capacity of logistic growth), were both typographical conveniences (Whitehead and Russell 1910) as well as population parameters with intrinsic meanings and qualities. Such numerical relationships were manipulated in greater detail until they were capable of predicting complex systems of interaction (i.e., the community matrix).

Trophic dynamics, genetics, mathematical ecology, and biogeochemistry all fell easily within the ecosystem topic area. The ecosystem was gradually being described in greater detail than merely species lists, community composition, or habitat characteristics. The application of mathematical models to ecological processes enabled complex sets of interactions to be represented in a manner similar to an electrical network. Accordingly, tools developed by electrical engineers, involving differential equations, were adopted to examine ecosystem dynamics.

At the same time, world events affected scientific research. The atomic bomb was developed, and so was the availability of radioactive tracers that enabled the ecosystem scientist, at last, to actually observe elemental transfers through the food web (network).

The advanced mathematical tools, radiotracers, and the development of increased computational power and computers combined to allow ecosystems to be quantified in a manner that was not possible only a few years earlier. But ideas, for the time being, led the technology. And ecosystem ecology expanded from descriptive studies to experimentation and prediction.

The two Odum brothers, as many other ecologists and scientists, were instrumental in this expansion. This period of new ideas and capability marks the beginning of modern ecosystem concepts. Among the others were Hutchinson (1948, 1953, 1959, 1964, 1965, 1975), Woodwell and Smith (1969), and O'Neill (1971, 1976).

Eugene Odum (1953, 1959, 1960, 1969, 1971, 1977) made ecology and the ecosystem a popular idea in the minds of the public. He and his brother, Howard Odum (1957, 1962, 1971, and 1983) brought ecological systems into social, economic, and political relevance.

With the development of computational methods and public awareness of real environmental problems, ecosystem concepts began to affect legislation and regulation. This was particularly true for aquatic systems where certain nutrients were implicated as pollutants.

Ecosystem Stability. With the emergence of ecosystem science and the modern concept of the ecosystem, the subject of ecosystem stability quickly received renewed attention. The concept of stability was an outgrowth of the mathematical work of A.M. Liapunov and a new ecological terminology was created by Holling (1970, 1973), Patten (1971-1976, 1978), Webster et al. (1975), Van Voris (1976), and Van Voris et al. (1980). There were others as well. Stability was considered an emergent property because mere description of individual populations could not predict the quality. Only when quantitative methods were applied to the system could stability be predicted mathematically.

An excellent reference that provides a critical view of this idea and many others in ecology is Peters (1991), which contains the following:

Despite long-standing interest in stability (Brookhaven Symposium 1969, May 1974) the term has never been satisfactorily defined. Part of the difficulty in doing so reflects the dynamism of open biological systems ...[they] constantly react to both external and internal changes...[and] cannot be preserved like works of art. Instead stability must be defined in dynamic terms. Such contradictions foster misunderstanding...The definitions of Orians (1975) are indicative. Orians (1975) suggests that stability may mean many different things: the absence of change ('constancy'), the length of survival ('persistence'), resistance to perturbation ('inertia'), speed of return after perturbation ('elasticity'), the displacement from which return is possible ('amplitude'), the degree of oscillation ('cyclic stability'), and the tendency to move towards a similar end point ('trajectory stability'). These independent concepts are sometimes related, and sometimes not (Orians 1975); some, like constancy and resilience, may even be inversely related.

The confusion pointed to by Peters (1991) remains today. For further definition of the various terms related to ecological stability, see Pimm (1991).

Applications and studies of the ecosystem concept. Because the ecosystem concept has now been broadly applied in scientific research and to the management of resource problems, it has an extensive literature. Only a brief introduction to this literature is provided here by way of some widely recognized (classic) applications of the concept. For example, students of ecosystem sciences should be aware of the Coweeta Basin and Coweeta Hydrologic Laboratory in North Carolina. This small, forested basin in the Appalachian Mountains was established as a research area in 1934 and is the longest, continuous environmental study in North America (Swank et al. 2001). Studies by Johnson, Swank, and a host of associates began at Coweeta in the 1960's and demonstrated the ecosystem approach to forested watersheds. These studies (e.g., Swank and Vose 1994; Swank and Waide 1980) used numerical models to predict the outcome of nutrient release and retention in a forested watershed dependent on a variety of management practices (Swank et al. 2001). This work had implications not only for forest management, but for land management in general and for impacts to receiving waters in particular. In a related development, the Hubbard Brook Experimental Forest in the White Mountains of central New Hampshire was established by the U.S. Forest Service in 1955 as a research site for forested watersheds in New England. Work begun in the 1970s and continued by Bormann and Likens and their numerous students and associates on Hubbard Brook itself, the surrounding forested basin, and the receiving waters of Mirror Lake, established the ecosystem approach as a major contributor to quantitative and theoretical ecology.

Complex vs. Simple Ecosystem Models. As the field of systems ecology began to emerge in the 1940s and to be applied to real ecological problems, a philosophical split began to develop between modelers that used the mathematical and computer methods of systems analysis (e.g. Kenneth Watt, Bernard Patten, Eugene Odum) and those that relied more on traditional mathematics (e.g., calculus and differential equations) to make analytical evaluations of system behavior (e.g. Richard Levins, E.O. Wilson, Richard Lewontin, and Robert McArthur). Those who used the traditional mathematical approaches were forced to greatly simplify the systems they considered so that they could be examined with "paper and pencil" (although computers were certainly used). This approach forced the investigator to discover (or assume) the overarching, fundamental properties of the system before proceeding, and if successful, would lead to results that could be understood and interpreted. Those that used this approach felt that the systems analyst's method was mechanical and unworkable; it often required measurements that were unattainable and many times produced results that could not be interpreted or compared to real observations. For their part, the systems analysts argued that complexity was the key to ecosystem behavior, and the analytical approach was fatally flawed by its omission of this complexity. They believed that increasingly powerful computers would allow systems ecology to transcend the limits of traditional analysis. As is usually the case, there are strong arguments (and advantages) to both approaches. The engineering models used by the USACE are direct descendants of the view espoused by the early systems analysts. Many biological-ecological models now fit that mold also, but the simplifying philosophy of the analytical approach is still active and has much to offer, particularly for its heuristic value. It is also interesting to note that some of the differences between the analytical and systems approaches can be framed, in least in part, as a difference in scale.

The arguments and counter-arguments for the analytical and systems approaches are described in several papers. Odenbaugh (2003) presents a good summary and perspectives on the controversy. In the original papers, the systems analyst approach is typified by Watt (1962,1966, 1968) and Orzack and Sober (1993), and the counter-view is represented by Richard Levins (1966, 1968, and 1993).

Balance and Control in Ecosystems. The classic paper by Slobodkin (1965) is as entertaining as it is informative, and it leads nicely into another exchange of views on the nature of ecosystem interactions and regulation. In this discussion, Hairston et al. (1960) throw down the gauntlet in the conflict between ‘top down’ organizational control of the ecosystem versus ‘bottom up’ control. In ‘top down’ control, predators control the numbers of lower trophic levels and ultimately how much sunlight is fixed by autotrophs into biomass. The ‘bottom up’ view supports the idea that producers control higher trophic levels. The proposals in Hairston et al. (1960) were subsequently criticized by Murdoch (1966). The entire series of papers, which includes Ehrlich and Birch (1967) and Slobodkin et al. (1967) is worth reading, but if time is limited, the first two are the most important.

Slobodkin et al. (1967) also mention the ‘Balance of Nature’ that is a common theme in the literature. However, this concept has been so poorly defined and employed for so many differing purposes that now it seems to have almost no practical utility. It is evident in much of the discussion on ecological stability that the “Balance of Nature” is an underlying notion of the Clementsian view of the community, and some elements of it have been codified into law (i.e. the so-called ‘balanced biological community’). None of these have been carefully identified or described and they are not available to objective examination. Therefore, the authors will not provide any further discussion of this topic.

Complex Adaptive Systems and “Superorganisms.” Complex systems of interacting biotic and abiotic components can appear to behave almost like a living thing in their response and adaptation to changing conditions. This has prompted some to propose that ecosystems were, in fact, ‘superorganisms.’ However, ecosystems do not seem to have an ability to behave like an organism with respect to evolutionary fitness, and this has led some to see the analogy between systems and organisms to be substantially flawed.

Succession and climax are important expressions of evolution and adaptation of species and communities. But the community level characteristics of successions and climaxes are consequences of the evolution of species and their interaction and function in relation to environmental constraints and resources,

...we know of no selective mechanism acting at the community level,” only at the level of the population (Whittaker and Woodwell 1972)

This statement of the problem was one of the first attempts to arrive at a solution, but there were others (Darnell 1970, Smith 1975, Lewontin 1970, Wilson 1976). Of these, Lewontin (1970) seems, in retrospect, to have been closer to progress than the others although all of them saw the problem and made good attempts at solutions. Approximately two decades later their ideas had been noticed and a new view of ecosystems was proposed – Complex Adaptive Systems.

The following titles address the idea that complex systems may be able to adapt (through coevolutionary and other mechanisms) to changing environments:

- Carpenter et al. (2001), “From metaphor to measurement: resilience of what to what?”
- Hartvigsen et al. (1998), “Use and analysis of complex adaptive systems in ecosystem science”
- Holling (2001), “Understanding the complexity of economic, ecological, and social systems”
- Janssen (1998), “Use of complex adaptive systems for modeling global change”
- Levin (1998), “Ecosystems and the biosphere as complex adaptive systems”
- Nystroem and Folke (2001), “Spatial resilience of coral reefs”
- Peterson et al. (1998), “Ecological resilience, biodiversity, and scale”
- Pickett and Cadenasso (2002) “The ecosystem as a multidimensional concept: meaning, model, and metaphor”

The complex adaptive systems described in these articles are ecosystems in every respect. But conceptually they are capable of real genetic adaptation as systems. In this concept, ecosystems again resemble superorganisms and real mechanisms for system adaptation are proposed. This approach could potentially impart dynamic properties to an ecosystem that allow it to be compatible with evolutionary theory. The consideration of an ecosystem as an evolving entity opens a new area for model application and predictive capacity. It would be a significant move beyond the relatively simple engineering approaches employed today, but this approach to ecosystems seems to imply scales of time and space (multiple centuries or millenia and continents) that reach beyond the considerations of most modern engineering projects.

SUMMARY AND COMMENT: The linking of models of physical-chemical drivers (engineering models) to models of biotic response (ecological models) is an exercise that must carefully address the issues of hierarchy, scale (in time and space), frameworks of reference, and currencies used by the candidate models. To understand the hurdles that must be surmounted in creating model linkages and to be a contributor to the model linkage effort, practitioners should have a basic understanding of ecosystem modeling and the ecosystem concept. The literature review and bibliography provided here are intended as an entry point for gaining an introductory grounding and a basic appreciation for this topic.

In well-conditioned situations, it is clearly possible and beneficial to link engineering models of drivers (the physical-chemical environment) to higher-level models of ecological response. Two examples (Peoria Lake and Richard B. Russell Lake) where this was successful for specific, restricted purposes are shown. The authors have also seen an example where such a linkage is proving extremely difficult (Chesapeake Bay) and can easily envision situations where it would be impossible or meaningless. Connections in two directions (to and from the biota), or with multiple hierarchical levels are far more difficult and are less likely to be successful without substantial changes to the underlying models. The actual details of transferring data from one model to another are beyond the scope of this presentation, but can be a tedious undertaking; one that may require additional computer code and ecological research to allow a meaningful connection. Experts who represent both sides of the proposed model linkage and the underlying ecological sciences must be involved in any linkage attempt. These experts will serve to (1) evaluate and resolve the conceptual issues involved in the linkage, and (2) design the actual linkage

mechanism. The linkage of two models is envisioned as a very model-specific undertaking that could yield enormous dividends to water resource managers in specific instances, but is not a simple, automatic process, and it should not be attempted without careful consideration and a well-demonstrated need.

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REFERENCES:

- Ahl, V., and T. F. H. Allen. 1996. *Hierarchy theory, a vision, vocabulary and epistemology*. Columbia University Press.
- Allen T. F. H., and T. Hoekstra. 1992. *Toward a unified ecology*. Columbia University Press.
- Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy: perspectives for ecological complexity*. University Chicago Press.
- Anker, P. 2002. The context of ecosystem theory. *Ecosystems* 5:611-613.
- Best, E. P. H., and W. A. Boyd. 2001. *VALLA (version 1.0): A simulation model for growth of American wildcelery*. ERDC/EL SR-01-1. Vicksburg, MS: U.S. Army Engineer Research and Development Center.
- Best, E. P. H., and W. A. Boyd. 2003. *POTAM (version 1.0): A simulation model for growth of Sago pondweed*. ERDC/EL SR-03-1. Vicksburg, MS: U.S. Army Engineer Research and Development Center.
- Best, E. P. H., A. H. Teeter, and S. K. Nair. 2004. *Modeling the impacts of suspended sediment concentration and current velocity on submersed vegetation in an Illinois River pool, USA*. APCRP Technical Notes Collection (ERDC TN-APCRP-EA-07). Vicksburg, MS: U.S. Army Engineer Research and Development Center. www.wes.army.mil/el/aqua
- Bormann, F. H., and G. E. Likens. 1979. *Pattern and process in a forested ecosystem*. Springer-Verlag. New York. 253 pp.
- Brookhaven Symposium in Biology. 1969. *Diversity and stability in ecological systems*. No. 22. Upton, NY: Brookhaven National Laboratory.

- Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From metaphor to measurement: Resilience of what to what? *Ecosystems* 4:765-781.
- Clements, F. E. 1916. *Plant succession*. Carnegie Institute Publication 242. Washington, D.C.: Carnegie Institute.
- Clements, F. E. 1928. *Plant succession and indicators*. New York: H.W. Wilson and Company.
- Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Bot. Gaz.* 27:95-117, 167-202, 281-308, 361-391.
- Cowles, H. C. 1901. The influence of underlying rocks on the character of the vegetation. *Bull. Am. Bur. Geog.* 2:1.
- Cowles, H. C. 1911. The causes of vegetative cycles. *Bot. Gaz.* 51:161-183.
- Darnell, R. M. 1970. Evolution and the ecosystem. *American Zoologist* 10:9-5.
- Darwin, C. R. 1859. *The origin of species by means of natural selection; or, the preservation of favored races in the struggle for life*. London: John Murray.
- Dobzhansky, T. 1973. Nothing in biology makes sense except in the light of evolution. *Am. Biology Teacher* 35:125-129.
- Ehleringer, J. R. and C. B. Field, eds. 1993. *Scaling physiological processes: Leaf to globe*. New York: Academic Press.
- Ehrlich, P. R., and L. C. Birch. 1967. The "Balance of Nature" and "Population Control." *The American Naturalist* 101:97-107.
- Fisher, R. A. 1930, revised 1958. *The genetical theory of natural selection*. Revised edition. New York: Dover Press.
- Flowers, R. B. 2002. *Environmental Operating Principles for the U.S. Army Corps of Engineers*. <http://www.hq.usace.army.mil/cepa/envprinciples.htm>
- Forbes, S. A. 1887. The lake as a microcosm. *Bull. Peoria Scientific Assoc.* 77-87. Reprinted in 1925. Illinois Nat. History Survey Bull. #15:537-550.
- Gleason, H. A. 1917. The structure and development of the plant association. *Bull. Torrey Botanical Club.* 44:463-481. Viewable online at: <http://www.jstor.org/view/00409618/di004625/00p41494/0>
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bull. Torrey Botanical Club.* 53:7-26. Viewable online at: <http://www.jstor.org/view/00409618/di004721/00p4707h/0>
- Gleason, H. A. 1939. The individualistic concept of the plant association. *Amer. Midlands Naturalist* 21:92-110.

- Golley, F. B. 1993. *A history of the ecosystem concept in ecology. More than the sum of the parts*. New Haven, CT: Yale University Press.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421-425.
- Harper, J. L. 1977. The contributions of terrestrial plant studies to the development of the theory of ecology. In: *The changing scenes in the natural sciences, 1776-1976*. Special Pub. 12. ed. C. E. Goulden, 139-157. Philadelphia, PA: Academy of Natural Sciences.
- Hartvigsen, G., A. Kinzig, and G. Peterson. 1998. Use and analysis of complex adaptive systems in ecosystem science: Overview of special section. *Ecosystems* 1:427-430.
- Heemskerk, M., K. Wilson, and M. Pavao-Zuckerman. 2003. Conceptual models as tools for communication across disciplines. *Conservation Ecology* 7(3): 8. [online] URL: <http://www.consecol.org/vol7/iss3/art8/>
- Holling, C. S. 1970. Stability in ecological and social systems. In: Symposium Brookhaven National Laboratory. BNL 50175(C-56), 128-141.
- Holling, C. S. 1973. Resilience and stability in ecological systems. *Ann. Rev. Ecol. Systematics*. 4:1-23.
- Holling, C. S. 2001. Understanding the complexity of economic, ecological, and social systems. *Ecosystems* 4:390-405.
- Hutchinson, G. E. 1948. Circular causal systems in ecology. *Ann. N.Y. Acad. Sci.* 50:221-246.
- Hutchinson, G. E. 1953. Concept of pattern in ecology. *Proc. Phila. Acad. Sci.* 105:1-12.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals. *American Naturalist* 93:155-160.
- Hutchinson, G. E. 1964. The lacustrine microcosm reconsidered. *Am. Scientist* 52:334-341.
- Hutchinson, G. E. 1965. *The ecological theater and the evolutionary play*. New Haven, CT: Yale University Press.
- Hutchinson, G. E. 1975. Variations on a theme by Robert MacArthur. In: *Ecology and evolution of communities*, ed. M.L. Cody and J.M. Diamond, 492-521. Cambridge, MA: Harvard University Press.
- Jackson, L. J., A. S. Trebitz, and K. L. Cottingham. 2000. An introduction to the practice of ecological modeling. *BioScience* 50:694-706.
- Janssen, M. 1998. Use of complex adaptive systems for modeling global change. *Ecosystems* 1:457-463.
- King, W. 1685. On the bogs and loghs of Ireland. *Phil. Trans. Roy. Soc. London* 15:948.

- King, A. W. 1991. Translating models across scales in the landscape. In M. G. Turner and R. H. Gardner, eds., *Quantitative methods in landscape ecology: The analysis and interpretation of landscape heterogeneity*, 479-517. New York: Springer-Verlag.
- Kormondy, E. J. 1965. *Readings in ecology*. Englewood Cliffs, NJ: Prentice-Hall, Inc.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.
- Levin, S. A. 1998. Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* 1:431-436.
- Levins, R. 1966. The strategy of model building in population biology. *American Scientist* 54: 421-431.
- Levins, R. 1968. Ecological engineering: theory and technology. *The Quarterly Review of Biology* 43; 3: 301-305.
- Levins, R. 1993. A response to Orzack and Sober: Formal analysis and the fluidity of science. *The Quarterly Review of Biology* 68, 4: 547-555.
- Lewontin, R. C. 1970. The units of selection. *Annual Review of Ecology and Systematics* 1:1-18.
- Lotka, A. J. 1925. *Elements of physical biology*. Baltimore, MD: Williams and Wilkins.
- McIntosh, R. P. 1985. *The background of ecology. Concept and theory*. Cambridge, UK: Cambridge University Press.
- Mobius, K. 1877. *An oyster-bank is a biocoenose, or a social community (Die auster und die austerwirthschaft)* Berlin, Germany: Wiegundt, Hempel, und Parey. Translated and reprinted in 1880 in 'Report of the U.S. Commission of Fisheries,' 683-751.
- Murdoch, W. W. 1966. Community structure, population control, and competition – a critique. *The American Naturalist* 100:219-225.
- Nestler, J. M., A. Goodwin, and L. T. Schneider. 2000. *Linking biological models and spatial descriptions of environmental complexity with coupled models*. EMRRP Technical Notes Collection (ERDC TN-EMRRP-EM-01). Vicksburg, MS: U.S. Army Engineer Research and Development Center. www.wes.army.mil/el/emrrp
- Nestler, J. M., R. A. Goodwin, and D. P. Loucks. 2005. Coupling of engineering and biological models for ecosystem analysis. *Journal of Water Resources Planning and Management* 131(2): 101-109.
- Nystroem, M., and C. Folke. 2001. Spatial resilience of coral reefs. *Ecosystems* 4: 406-417.
- Odenbaugh, J. 2003. Complex systems, trade-offs, and theoretical population biology: Richard Levin's "Strategy of Model Building in Population Biology" revisited. *Philosophy of Science* 70: 1496-1507.

- Odum, E. P. 1953. *Fundamentals of ecology*. Philadelphia, PA: W.B. Saunders.
- Odum, E. P. 1960. Organic production and turnover in old field succession. *Ecology* 41:34-49.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* 164:262-270.
- Odum, E. P. 1971. *Fundamentals of ecology (3rd edition)*. Philadelphia, PA: W.B. Saunders.
- Odum, E. P. 1977. The emergence of ecology as a new integrative discipline. *Science* 195:1289-1293.
- Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.* 27:55-112.
- Odum, H. T. 1962. The use of a network energy simulator to synthesize systems and develop analogous theory: The ecosystem example. In: *Proceedings of the Cullowhee Conference on Training in Biomathematics*. ed. H.L. Lucas, Raleigh, NC: Institute of Statistics, N.C. State Univ.
- Odum, H. T. 1971. *Environment, power, and society*. New York: Wiley-Interscience.
- Odum, H. T. 1983a. *Systems ecology: An introduction*. New York: John Wiley & Sons.
- Odum, E. P. 1983b. *Basic ecology*. New York: Saunders College Publishing.
- O'Neill, R. V. 1971. Examples of ecological transfer matrices. Oak Ridge National Laboratory. ORNL-IBP-71-3.
- O'Neill, R. V. 1976. Ecosystem persistence and heterotrophic regulation. *Ecology* 57:1244-1253.
- O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. *Monographs in Biology, No. 23*. Princeton, NJ: Princeton University Press.
- O'Neill, R. V., and A. W. King. 1998. Homage to St. Michael; or, why are there so many books on scale? In: *Ecological Scale: Theory and Applications*, ed. D. L. Peterson and V. T. Parker. Columbia University Press.
- Orians, G. 1975. Diversity, stability and maturity in natural ecosystems. In: *Unifying Concepts in Ecology*. ed. W. H. Van Dobben and R. H. Lowe-McConnell. Dr. W. Junk, The Hague.
- Orzack, S. H., and E. Sober. 1993. A critical assessment of Levins' The Strategy of Model Building in Population Biology. *The Quarterly Review of Biology* 68, 4: 533-546.
- Patten, B. C. 1971-1976. Systems analysis and simulation in ecology, Vols. 1-4. New York: Academic Press.
- Patten, B. C. 1978. Systems approach to the concept of the environment. *Ohio J. Sci.* 78:206-222.

- Peters, R. H. 1991. *A critique for ecology*. Cambridge, UK: Cambridge University Press.
- Peterson, D. L., and V. T. Parker, ed. 1998. *Ecological scale: Theory and application*. Columbia University Press.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity, and scale. *Ecosystems* 1:6-18.
- Pickett, S. T. A., and M. L. Cadenasso. 2002. The ecosystem as a multidimensional concept: Meaning, model, and metaphor. *Ecosystems* 5:1-10.
- Pimm, S. L. 1991. *The Balance of Nature?* Chicago, IL: University of Chicago Press.
- Real, L. A., and J. H. Brown. 1991. *Foundations of ecology. Classic papers with commentaries*. Chicago, IL: University of Chicago Press.
- Rosswall, T., R. G. Woodmansee, and P. G. Risser, eds. 1988. *Scales and global change*. New York: John Wiley and Sons.
- Schneider, D. C. 1994. *Quantitative ecology. Spatial and temporal scaling*. Academic Press.
- Shugart, H. H. 1990. Ecological models and the ecotone. In: *The ecology and management of aquatic-terrestrial ecotones. Man and the biosphere series, Vol. 4*. ed. R. J. Naiman and H. Decamps, 23-36. Paris, France: UNESCO.
- Slobodkin, L. B. 1965. On the present incompleteness of mathematical ecology. *American Scientist* 53:347-357.
- Slobodkin, L. B., F. E. Smith, and N. G. Hairston. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. *The American Naturalist* 101:109-124.
- Smith, F. E. 1975. Ecosystems and evolution. *Bull. Ecol. Soc. Am.* 56:2-6.
- Swank, W. T., and J. M. Vose. 1994. *Forest hydrology and ecology at Coweeta*. New York: Springer-Verlag.
- Swank, W. T., and Waide, J. B. 1980. Interpretation of nutrient cycling research in a management context: Evaluating potential effects of alternative management strategies on site productivity. In: *Forests: fresh perspective from ecosystem analysis*, 137-158. Corvallis. OR.
- Swank, W. T., J. L. Meyer, and D. A. Crossley, Jr. 2001. Long-term ecological research: Coweeta history and perspectives. In: *Holistic Science*, ed. G. W. Barrett and T. L. Barrett, 143-163. Ann Arbor, MI: Sheridan Books.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:284-307. viewable online at: <http://www.jstor.org/view/00129658/di960063/96p00052/0>

- Taylor, P. 2000. Socio-ecological webs and sites of sociality: Levins' strategy of model building revisited. *Biology and Philosophy* 15:197-210.
- Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. *Landscape ecology in theory and practice: pattern and process*. New York: Springer.
- U.S. Environmental Protection Agency. (USEPA). 2005. *Coupling water quality and upper trophic level models for Chesapeake Bay: A planning workshop. January 8-9, 2004, Annapolis, Maryland*. U.S. Environmental Protection Agency Chesapeake Bay Program, Science Technical Advisory Committee Publication 05-002.
<http://www.chesapeake.org/stac/workshop.html>
- Van Voris, P. 1976. *Ecological stability: An ecosystem perspective – Classical and current thought. A review of selected literature*. Oak Ridge National Laboratory. ORNL/TM-5517.
- Van Voris, P., R. V. O'Neill, W. R. Emanuel, and H. H. Shugart. 1980. Functional complexity and ecosystem stability, an experimental approach. *Ecology* 61:1352-1360.
- Vande Castle, J. 1998. Remote sensing applications in ecosystem analysis. In: *Ecological scale: Theory and applications*, ed. D. L. Peterson and V. T. Parker. Columbia University Press.
- Warming, J. E. B. 1895. *Plantensamfund* (Revised for English edition as "Oecology of plants," 1909). Oxford, UK: Clarendon Press.
- Warming, J. E. B. 1909. *Oecology of plants: An introduction to the study of plant communities*. Oxford, UK: Oxford Univ. Press.
- Watt, K. E. F. 1962. Use of mathematics in population ecology. *Annual Review of Entomology* 7: 243-260.
- Watt, K. E. F. 1966. *Systems analysis in ecology*. New York: Academic Press.
- Watt, K. E. F. 1968. *Ecology and natural resource management*. McGraw Hill.
- Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient recycling and the stability of ecosystems. In: *Mineral recycling in southeastern ecosystems*. ERDA Con F-74-513. ed. G. Howell, J. B. Gentry, and M. H. Smith. National Technical Information Service. U.S. Dept. Commerce.
- White, I. D., D. N. Mottershead, and S. J. Harrison. 1992. *Environmental systems: An introductory text*. Chapman and Hall.
- Whitehead, A. N., and B. Russell. 1910. *Principia mathematica. Vol. I*. Cambridge, UK: Cambridge University Press.
- Whittaker, R. H. 1975. *Communities and ecosystems*. New York: Macmillan Publishing Co, Inc.

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Whittaker, R. H., and G. M. Woodwell. 1972. Evolution of natural communities. *Ecosystem structure and function*, 137-159.

Wilson, D. S. 1976. Evolution on the level of communities. *Science* 192:1358-1360.

Woodwell, G. M., and H. H. Smith ed. 1969. Diversity and stability in ecological systems. *Book-haven Symp. Biol.* No. 22.

Worster, D. E. 1977. *Nature's economy*. San Francisco, CA: Sierra Club Books.