Norton, B.G. 1989. Intergenerational equity and environmental decisions: a model using Rawls' veil of ignorance. *Ecological Economics*, 1:137-159.

RAAS. 1989. *Towards an Ecosystem Charter for the Great Lakes - St. Lawrence.* The Rawson Academy of Aquatic Science, Ottawa, Ontario, iv + 112 pp.

Rapport, D.J. and H.A. Regier. 1992. Disturbance and stress effects on ecological systems. In: B.C. Patten (ed.). *Complex Ecology: the Part-Whole Relation in Ecosystems.* Prentice-Hall, New York. (In press).

Regier, H.A. and A.L. Hamilton. 1990. Towards ecosystem integrity in the Great Lakes-St. Lawrence River Basin, pp. 182-196. In: J.O. Saunders (ed.). *The Legal Challenge of Sustainable Development.* Canadian Institute of Resources Law, Calgary, Alberta, x + 401 pp.

Regier, H.A., P. Tuunainen, Z. Russek and L.E. Persson. 1988. Rehabilitative redevelopment of the fish and fisheries of the Baltic Sea and the Great Lakes. *Ambio*, 17:121-130.

Sagoff, M. 1988. *The Economy of the Earth.* Cambridge University Press, Cambridge, U.K., x + 271 pp.

Ulanowicz, R.E. 1986. *Growth and Development: Ecosystems Phenomenology.* Springer-Verlag, New York, xiv + 203 pp.

Van Hise, C.R. 1911. *The Conservation of Natural Resources in the United States.* The MacMillan Company, New York, U.S.A. xi + 413 pp.

Woodwell, G.M. 1977. Biological integrity - 1975. pp. 141-148. In: R.K. Ballentine and L.J. Guarraia (eds.). *The Integrity of Water.* U.S. Government Printing Office, Washington, D.C. No. 055-001-01068-1. vi + 230 pp.

Considerations of Scale and Hierarchy

ANTHONY W. KING
Environmental Sciences Division, Oak Ridge National Laboratory
Oak Ridge, Tennessee

Introduction

Explicit considerations of scale are increasingly a part of the process by which ecologists approach a variety of ecological issues and problems, and hierarchy theory is commonly used to address questions of scale. Thus, it is expected and appropriate that the evolving issues of monitoring and managing ecosystem integrity be concerned with questions of scale and hierarchy.

How do considerations of scale and hierarchical organization influence the measurement or management of ecosystem integrity? What considerations of spatial and temporal scale should go into the design of measures for ecosystem integrity? Answers to these questions first require some definitions. What is ecosystem integrity? What is an ecosystem? And what are scale and hierarchical organization in these ecosystems?

The Ecosystem Concept

Ecosystem As Entity

The concept of ecosystem is both widely understood and "diffuse and ambiguous" (O'Neill *et al.* 1986). The ecosystem may be specific or generic, referring to a particular ecosystem or some ecosystem type. There are references to the Cedar Bog Lake ecosystem (Williams 1971), the Isle Royale National Park ecosystem (Rykiel and Kuenzel 1971), Great Lakes ecosystems (Magnuson *et al.* 1980), the Hudson River ecosystem (Limburg *et al.* 1986), the Serengeti ecosystem (Sinclair and Norton-Griffiths 1979), southeastern [United States] ecosystems (Howell *et al.* 1975), forest ecosystems (Reichle 1981), tropical rain forest ecosystems (Golley 1983), an oak ecosystem (Zak and Pregitzer 1990), and a *Populus tremuloides* ecosystem (Ruark and Bockheim 1988). The ambiguity in this use of ecosystem is

understood, and *ecosystem* is a useful handle for referring to "that ecological stuff out there, over there."

Ecosystem is variously defined as the collection of all the organisms and environments in a single location (Tansley 1935, McNaughton and Wolf 1979), any organizational unit, including one or more living entities, through which there is a transfer and processing of energy and matter (Evans 1956), or a system, i.e., a collection of interacting components and their interactions, that includes ecological or biological components (Lindeman 1942, Odum 1971, 1983, Golley 1983). Interactions in these latter ecosystems are through transfers of energy and matter (Odum 1983). Common to all these definitions, and at least implicit in the general usage described above, is the idea that the ecosystem includes the physical or abiotic environment in addition to biological components (e.g., organisms). Inclusion of the physical environment distinguishes the concept of ecosystem from that of community. Community generally refers to the assemblage of species or populations in a location without explicit reference to their physical environment.

Strongly associated with the concept of ecosystem is the concept of *ecosystem function*. Ecosystem function generally refers to the functioning or operation of the ecosystem, its integrated holistic dynamics, and not the role or job of the ecosystem. The distinction is analogous to the difference between the functioning of an automobile and its function as a means of transportation. Ecosystem function is commonly associated with the dynamics of matter and energy processing and transfer. Biomass production and nutrient cycling, for example, are often referred to as ecosystem functions.

The concept of ecosystem function is implicit in the general use of ecosystem to refer to the collective ecology of a given location. There is a tendency to include the term ecosystem when attention is given to dynamics of biota-biota or biota-environment interactions and not just simply the area's biotic composition or structure. Consider the reference to *forest ecosystem*, for example, rather than simply *forest*. Minimally, use of ecosystem in this context implies a consideration of both the biology and physical (abiotic) environment of an area and a consideration of dynamic interactions among biota and between biota and environment.

Ecosystem structure commonly refers to the distribution of matter and energy among system components. Because of the emphasis on function, ecosystem components are frequently defined by their functional roles, especially their rate controlling attributes. The structural components may, for example, be biota-environment aggregates with common turnover times or rates of matter-energy processing. Ecosystem carbon pools may be distinguished by turnover times (e.g., rates of decay) without separating dead organic matter from the microbial populations that feed on it.

Descriptions of ecosystem structure frequently do not consider the distribution of matter or energy among populations or species. Normally (perhaps mistakenly from the perspective of system science) a middle ground is taken in which biological components are grouped *a priori* according to a mix of criteria including functional roles, morphological types, distributions in time and space, and occasionally coarse taxonomic distinctions. For example, in describing the carbon structure of a forest ecosystem, autotrophs (photosynthetic plants) may be distinguished from heterotrophs. The autotrophs may be further divided into trees and non-trees of overstory and understory. The trees may be yet further divided into deciduous and evergreen forms. Adding function to this structure requires an assignment of carbon transfers and turnover times to these otherwise defined components. Ideas of structure precede those of function. But even in these cases, the concept of ecosystem function often influences the choice of components. Deciduous and evergreen trees are distinguished rather than angiosperms and gymnosperms. Foliage morphology and behaviour influence ecosystem carbon flux, and there is sufficient overlap in these traits between the two broad taxonomic groups to necessitate the alternative differentiation by lifeform.

Ecosystem structure associated with matter and energy transfer rarely involves even broad taxonomic distinctions much less Latin binomials. There are, however, important exceptions to this generality. The individual-based models of biomass growth and succession in forests are good examples (Botkin *et al.* 1972, Shugart and West 1977, Shugart 1984, Post and Pastor 1990). These models distinguish individuals by species, but they also assign species (individuals) to functional types defined by their response to the physical environment (e.g., shade or drought tolerance; Shugart 1984). In general, the greater the focus on biotic interactions or dynamics like competition or species turnover (e.g., succession), the greater the tendency to distinguish ecosystem components by species nomenclatures. The individual organism-based models of forest growth explicitly treat competition between individual trees. They also consider the consequences of these interactions for successional changes in ecosystem attributes generally associated with ecosystem function (e.g., primary productivity and turnover in soil organic matter and nutrients; Pastor and Post 1986, 1988). This duality is reflected in the models' mixed distinction of ecosystem components by taxonomic and functional criteria.

Ecosystem as Perspective

A distinction can be made between a population-community approach to ecosystems and a process-functional approach (O'Neill *et al.* 1986). The

former emphasizes species populations and interactions among them like competition and predation. The latter emphasizes the transfer and processing of matter and energy. In the population-community approach, the physical environment is seen as external to the system of biota and biotic interactions. In the process-functional approach the environment is an integral part of the system. In the extreme this dichotomy emerges as a distinction between community — the system of populations — and ecosystem—the system of matter-energy transformations through biota and environment. The separation of community and ecosystem ecology in textbooks and classrooms is evidence of the acceptance of this dichotomy.

Note, however, that both approaches emphasize interactions. One emphasizes biotic interactions, the other fluxes of matter and energy. Thus *ecosystem* may be identified as a perspective, a particular way of looking at the biota and environment of an area. *Community* is a different perspective. Alan and Hoekstra (1990) refer to these perspectives as criteria for distinguishing foreground from background, and for distinguishing an object from its context. The ecosystem criteria distinguishes fluxes of material and energy; the community criteria distinguishes collections of species. Allen *et al.* (1984) discuss the observer's choice of phenomena, the structurally defined entities that are designated as significant. In systems science these perspectives are criteria for system specification. They are criteria for the definition of observables (Rosen 1977). The investigator chooses to order, describe, and observe the system of biota and environment according to one of these perspectives. The ecosystem is not ontologically different from the community, they are simply different ways of looking at the same "stuff."

Ecosystem as a Hierarchical Level

The ecosystem is often identified as one level in an ecological or biological hierarchy extending from cells to biosphere (e.g., Odum 1971, Krebs 1978). This "traditional" (O'Neill *et al.* 1986) or "conventional" (Allen and Hoekstra 1990) hierarchy is an ordering based on structural organization. A collection of entities at one level is organized to form the next higher level. Cells are organized as organs, organs as organisms, organisms as populations, and populations as communities. According to this concept of ecosystem, the ecosystem is a higher level of organization than the community, and ecosystems contain communities just as organisms contain cells. The concept of ecosystem as level is pervasive, and there is frequent reference to the ecosystem level (Rapport *et al.* 1985) or ecosystem-level properties (Rapport *et al.* 1985, Huston *et al.* 1988, Clark 1990).

The concept of ecosystem as hierarchical level is counter to the concept of ecosystem as perspective or observational criterion. In the perspec-

tive concept, ecosystems are not composed of communities. Ecosystem and community are instead complementary descriptions of the same ecological system (O'Neill *et al.* 1986, Allen and Hoekstra 1990).

A consequence of the traditional hierarchical view of ecosystems is the idea that ecosystems are larger than the communities they contain, just as organisms must be larger than the cells they contain. It is generally recognized that an ecosystem may be large or small (e.g., there is usually no objection to referring to the cow-rumen ecosystem), but the generality emerges that ecosystems are larger scale than communities or populations. By this argument, ecosystem (ecosystem-level) processes or properties are larger scale than community processes or properties. This idea has inadvertently been reinforced by recent considerations of scale and hierarchy in ecological systems (Allen and Starr 1982, O'Neill *et al.* 1986). These discussions generally assert that higher levels of hierarchical organization are larger (or coarser) scaled than lower levels. Higher levels occupy larger spatial extents and are characterized by larger time constants (e.g., slower rates or longer turnover times). Starting with the idea that the traditional ecosystem level is a higher level than the community level, it would seem to follow ecosystems and ecosystem processes are larger scale than communities and community processes.

Allen and Hoekstra (1990) caution against confusing conventional levels of organization with hierarchical levels defined by considerations of time and space scales. O'Neill *et al.* (1986) similarly caution against confusing traditional levels of organization with hierarchical levels distinguished by differences in rates. They point to the paradox generated by recognizing that traditional community processes, like succession, may be much slower than traditional ecosystem processes like nutrient processing. Similarly, the spatial scales of nutrient cycling processes (e.g., microbial decomposition) may be much smaller than the spatial scale of the community defined by a species-area curve (O'Neill *et al.* 1986). Allen and Hoekstra (1990) argue that the confusion and apparent paradoxes can be avoided by recognizing that the ecosystem is actually only one of several possible criteria for ordering observations across a range of spatial and temporal scales and not a scale-defined level. O'Neill *et al.* (1986) argue that observations on an ecosystem, from either the process-functional perspective or the population-community perspective, can be ordered by various criteria to form alternative, complementary hierarchical structures. In short, the concepts of ecosystem and ecosystem properties like ecosystem integrity are not limited to a particular hierarchical level or to particular space and time scales. An ecosystem exists across a range of scales and may include several hierarchical levels.

To summarize, an ecological system is a system description of the interacting biota and environment of some time-space domain (some

place over some time period). Whether this system description distinguishes individuals or populations and interactions like competition (which transfer information among components) or functional components and the transfer of matter-energy is secondary to the primary concept that the ecosystem is a system. *Ecosystem* may be used as shorthand for ecological system (Odum 1983), but it should be remembered that for many, myself included, the term *ecosystem* invokes a biased view towards a system of matter or energy transfer, or a process-functional perspective. Nevertheless, in this chapter I will use *ecosystem* to refer to the most general notion of an ecological system occupying a particular place (and time), without regard to the specific criteria for system specification or ordering of observations.

Inclusion of the physical environment is a definitive element of the ecosystem concept. However, the environment may be represented by boundary conditions or external forces and does not necessarily have to be included as interactive system components. Thus, it is possible to refer to an ecosystem which includes the physical environment but, is defined by community criteria emphasizing populations and population interactions like competition.

The concept of *ecosystem* applies across hierarchical levels of organization and is not limited to the "ecosystem level" of the traditional hierarchy. Thus, an ecosystem may contain several hierarchical levels. Similarly, the concept of *ecosystem* is not limited to certain time or space scales (e.g., large scales), and an ecosystem may span a large range of spatial and temporal scales.

Ecosystem Integrity

Ecosystem Integrity As System Integrity

Integrity (excluding the notion of firm adherence to a code of conduct or behaviour) generally refers to the soundness or completeness of something, the state of being whole and unimpaired. The notion of ecosystem integrity is intuitively appealing and understandable. We wish our ecosystems to be sound, whole, and unimpaired, and we understand, intuitively, what it means for an ecosystem to be in that state. However, monitoring, managing, quantifying, analyzing, or legislating ecosystem integrity requires a more precisely defined, more objective or empirical, concept of ecosystem integrity. This is the aspect of ecosystem integrity that I address here.

Because an ecosystem is, I believe, first and foremost a system, it is proper to address ecosystem integrity from the perspective of system

integrity. What then is the system's, and thus ecosystem's, state of being whole and unimpaired?

A system is defined both by its components and the interactions among them. Similarly, a system description simultaneously involves both structure and function—what are the components, how are they connected, and how do they operate together? System integrity thus implies the integrity of both system structure and function, a maintenance of system components, interactions among them, and the resultant behaviour or dynamic of the system (e.g., succession or the processing of energy).

Strictly speaking, loss of any system component or any change in interactions can be viewed as a loss of system integrity. The system is no longer whole; something is missing or displaced. Thus, the loss of even a single species or population (a structural component) could be viewed as a loss of ecosystem integrity. However, it appears to me that, to a considerable degree, the intuitive concept of ecosystem integrity is biased towards functional integrity, the state of being unimpaired. There is a bias towards the integrity of ecosystem function, a maintenance of the whole system's integrated dynamic.

Function is often a consequence of structure and therefore, a change in structure may alter function. Obviously, loss of all primary producers (a structure defined by function) has dire consequences for ecosystem function. Similarly, loss of a "keystone" species (e.g., Paine's [1966] starfish) can influence ecosystem function, and invasion by exotic species (an addition of structure) can, in some circumstances, alter ecosystem function (Vitousek 1986). However, many systems, including ecological systems, are amazingly resilient to alteration of structure. Whole system function is maintained despite the structural change. Changes in structure (components or interactions) may often have little, or very transient, impact on system function. For example, when system components are organized in parallel, loss of one or more components is often compensated for by a redirection of flow through remaining parallel components. Parallel structure in ecosystems is related to the idea of functional redundancy or functional equivalence. Ecosystem components (e.g., species) may perform equivalent functions (i.e., operate in parallel), and loss of one or more may produce very little change in whole system function (O'Neill *et al.* 1986, Vitousek 1986). Primary productivity or nutrient cycling may, for example, remain relatively constant while species composition changes (Harcombe 1977, Rapport *et al.* 1985) or dominant species are removed (Foster *et al.* 1980).

Systems may also possess more active mechanisms of resilience. Feedback loops in interactions among system components may compensate for structural changes in such a way that whole system function is maintained or quickly restored. Systems may thus show adaptation to

structural change or even exhibit healing or recuperative powers. These kinds of responses are widespread and their existence readily accepted in clearly homeostatic systems like organisms (indeed the responses may be definitive). Ecosystems, may exhibit similar responses (Rapport *et al.* 1985), though some argue that these responses are only apparent or, at best, analogous to the responses of "truly" homeostatic systems.

The Dependency on Perspective

A change in structure, with little or no change in function, might be viewed as an insignificant loss of ecosystem integrity. If, however, the focus is primarily on ecosystem function, the change may not be considered a loss of ecosystem integrity at all. A classic example is a change in biodiversity (e.g., species richness) that produces no observable change in ecosystem function (e.g., primary productivity). Is the species loss an insignificant loss of integrity, or is it even appropriate to consider the change as a loss of integrity? Is there a loss of integrity if there is no consequence for ecosystem function?

Once again we are faced with the problem of perspective, the criteria for system identification and the ordering of observations. Changes in a system defined by one criteria may have little impact on observations of that same system defined by other criteria. Consider the extreme case posed by ecosystem perspectives involving aesthetic, ethical, or economic criteria. From these perspectives, the human observer is an integral part of the system. There is a flow of resource, value, or other currency between human and non-human components. The human is part of system function. The role may be passive, only receiving from the rest of the system (e.g., an aesthetic perspective), or the role may be active, receiving from and influencing system function (e.g., an economic or natural resource perspective). These perspectives can yield legitimate system descriptions, but they impart value to system components differently than more traditional scientific perspectives in which the human is not an integral part of the system. Translating ecosystem integrity defined from one perspective to notions of integrity for another can be problematic.

Forested ecosystems, for example, can recover from even extensive disturbance by fire or logging operations. The integrity of the system as a forest may be wholly retained (i.e., it returns to forest and not grassland or scrub) and species composition may change only slightly (although the distribution of biomass by species may be altered for some time). However, the aesthetic quality of the system may be severely damaged for much of the recovery period. The integrity of the system defined by "aesthetic interaction" with the biota has been lost. But has the integrity of the forest as a forest been compromised?

Consider also that rare species are often assigned the highest value or priority for preservation or use as indicator species. The attention given to rare species arises, in part, from the observations that rarity may be a consequence of declining populations in response to stress and rare species may be more at risk. These observations arise from a community perspective. There is also an aesthetic element. Humans are attracted to and value the rare or unique. Yet, in either case, because they are rare, rare species are unlikely to have much impact on ecosystem function (admitting the possibility of rare "keystone" species). The common species are more likely to be doing the brunt of the work in ecosystem function. Thus, while the persistence of rare (or endangered) species is a legitimate measure of integrity from a community (or aesthetic ethical) perspective, the persistence of common species may be more crucial to the ecosystem's functional persistence and integrity, and they may thus be more appropriate indicators of ecosystem functional integrity.

However, ecosystem function is often remarkably resilient to the loss of even common species. Witness the limited change in biomass dynamics of southern Appalachian forests following the demise the American chestnut, a formally common species (Shugart and West 1977, McCormick and Platt 1980). And what changes in North American ecosystems can be attributed to the loss of the once abundant carrier pigeon? Direct measures of functional properties (e.g., nutrient export [O'Neill *et al.* 1977]) may thus be more sensitive (better? appropriate?) measures of ecosystem functional integrity (O'Neill *et al.* 1977), but they, in turn, may be insensitive measures of the integrity of species composition.

Assessment of ecosystem integrity is strongly dependent upon the perspective from which observations are organized. Definitions and measures of ecosystem integrity from one perspective may complement, contradict, or be largely independent of those from other perspectives. Care must therefore be taken to define the perspective used in making statements about ecosystem integrity and in making inferences about integrity from other perspectives.

The strongest inference can be made by explicitly examining the integrity of alternative, complementary descriptions of an ecosystem. The work of Rapport *et al.* (1985) is a good example. Their recognition of a general ecosystem stress syndrome (i.e., a loss of integrity) includes indicators from both ecosystem and community perspectives (e.g., nutrient leaking and loss of biodiversity, respectively). But, even here, the perspectives are limited to those of "natural" ecosystems largely exclusive of the human component. Indicators of ecosystem integrity should include indicators from as many different perspectives and system descriptions, as practical. Those associated with human value judgements, like economics or aesthetics, should not be excluded by a prejudice for natural, ecological, or scientific perspectives.

Scale and Ecosystem Integrity

The scale of an ecosystem refers to the spatial and temporal dimensions of the ecosystem. How large an area does the ecosystem occupy, and over what time period does the system description pertain? Scale may also refer to the scale of the observation set used to define and describe the ecosystem. Here, scale includes concepts of both grain and extent (Allen *et al.* 1984, Turner and Gardner 1991). Grain is the finest level of temporal or spatial resolution in an observation set. The grain of an observation set determines the lower limit on how fine a distinction can be made with that observation set. Extent is the areal expanse or the length of time over which observations with a particular grain are made. Extent sets an upper limit on the distinctions that can be made with a particular observation set.

Specification of scale is a fundamental part of system definition (Levin 1975, Allen *et al.* 1984, O'Neill *et al.* 1986). The choice of scale, both grain and extent, with which a system is observed is a primary determinant of the resulting system description. Observations over one hectare and one year will lead to a different system description than observations over thousands of hectares and tens of years. Different extents encompass different components and interactions. Similarly, observations of different grain resolve different components, interactions, and dynamics. Once the scale of observation is chosen, the ensuing system description is largely determined. Consequently, those characteristics of ecosystem integrity which may be observed or inferred are largely determined.

The scale of an observation set used to define a system and measure ecosystem integrity may be determined by the scale of management units. I might for example wish to monitor or measure the integrity of the Great Smokey Mountains National Park ecosystem. My observations might then be limited to the spatial extent defined by the park boundary. It may be possible to construct a legitimate system description from observations within those boundaries, but the system description will be limited to the system existing over scales less than, or equal to, the extent of the management unit. I can make legitimate inferences about that system, but the limited extent of the observation set may not allow valid measurement or inference about those ecosystem attributes for which measures of integrity are truly desired and which may actually be attributes of a larger system. The extent of the observation set must be matched to the system attributes of interest. Specifically, the extent of the observation set must be larger than, or equal to, the extent of the system in question.

Systems require certain spatial and temporal extents for maintenance of system structure and function. A minimum extent may be required for

some process to operate or interaction to take place. For example, gap-phase forest dynamics occur at the spatial and temporal scales of dominant canopy trees (Shugart 1984). Similarly, the trophic interactions of wolves, moose, and vegetation on Isle Royale are played out over particular space and time scales. Failure to observe the system at these scales can obscure system structure and function and make inferences about ecosystem integrity difficult or impossible. Furthermore, restricting the system to an extent less than the minimum required for interactions to occur can impact system function and may lead to a loss of ecosystem integrity. Fences may physically impede the flow of interactions in the spatially distributed system (witness the impact of agriculture and fencing on African steppe ecosystems) and management units (e.g., park boundaries, state lines) may isolate the influence of management practices to scales less than sufficient to maintain system integrity. Clearly, the area required to manage wolf populations can be much larger than that needed to manage the persistence of an endangered bog plant, and it may exceed the boundaries of politically defined management units. The extent of the observation set required to measure the integrity of the ecosystem supporting North American waterfowl populations is larger than the extent of any single management unit. The example of innovative management scales and practices required for the management of migratory waterfowl populations can be extended to other ecosystem components.

Ecosystem integrity is a scale-dependent concept. Maintenance of ecosystem integrity implies maintenance of some normal state or norm of operation (e.g., homeostasis or homeorhesis). Measuring or observing ecosystem integrity, or its loss, thus requires observations over sufficient temporal extent to identify and characterize this normalcy. We are prisoners of perspective, and our concept of normal is empirically bound to the scales with which we observe a system. Long term observations may reveal slow changes in a system component identified as constant with short term observations. Similarly, observations over a large area can reveal heterogeneity imperceptible from limited, local observations. Concepts of normalcy, constancy, variability, and thus, ecosystem integrity are only meaningful within bounds set by the scale of observation.

Fire or other disturbance, for example, is often revealed as a normal part of ecosystem operation and seen as necessary for the maintenance of ecosystem integrity when the system is viewed from a long term, large scale, perspective. Locally and in the near term, fire can thoroughly destroy all integrity of system structure and function (e.g., change in canopy architecture, species composition, and productivity). But the persistence of the ecosystem, its larger scale integrity, may in fact depend on the recurrence of these catastrophic smaller scale losses of integrity (Vogl 1980). Similarly, observed changes in species composition might be seen

as indicating a loss of ecosystem integrity until a larger scale, longer term perspective reveals that these changes are part of a natural sequence of succession.

Hierarchy and Ecosystem Integrity

In simplest terms, a hierarchy is a ranked ordering. It generally implies a ranking by authority or dependency, but there are also static hierarchies (e.g., a hierarchy of size). As it applies to systems, a hierarchy is a ranked ordering of interactions. Control hierarchies are orderings of control, which system components control and are controlled by others (e.g., pecking orders, military command structures, or robotic controls). Structural hierarchies are orderings of subsystems within systems which are themselves parts of systems (Walters 1971). The organization of cells within organs, within organisms and squads within platoons, within companies are examples of structural hierarchies. Structural hierarchies generally exhibit some characteristics of control hierarchies (e.g., cell behaviour is normally constrained or controlled by its inclusion in the organism), but a system element can exhibit control beyond control over its component parts. For example, the control exerted by the alpha male in a baboon troop does not require that the alpha male be built of subordinate individuals. Thus, the distinction is sometimes drawn between nested (structural) hierarchies and non-nested (control) hierarchies (Allen and Starr 1982).

Systems can be ordered into hierarchies according to various criteria (O'Neill et al. 1986). Observations may be ordered by differences in rates, by tangible components, by spatial discontinuities, by traditional levels of organization, or even by arbitrary characteristics (e.g., colour). These alternative criteria lead to alternative hierarchical structures. Many of the criteria converge on similar structure (the robust transformation of Allen et al. 1984), and it has been suggested that rates may be a fundamental way of decomposing hierarchical structure (O'Neill et al. 1986). However, concepts, expectations, or predictions developed for hierarchies defined by one ordering criteria do not necessarily, or normally, transfer to hierarchies defined by other criteria (Allen et al. 1984). One must be careful to identify the ordering criteria involved.

There has been considerable discussion of hierarchy theory as it applies to ecological systems (Overton 1972, 1975, Webster 1979, Shilov 1981, Allen and Starr 1982, Patten 1982, Allen et al. 1984, O'Neill et al. 1986). This is not the place to attempt a review of that material. Rather, I will discuss aspects of nested hierarchies ordered by difference in rates that are particularly germane to the present discussion of ecosystem integrity. Much of the following discussion is drawn from O'Neill et al. (1986).

In a nested hierarchical system ordered by differences in rates, a level is identified by a distinct cluster of similar rates. Higher levels are characterized by slower rates. As a consequence of the physical nesting of structure, higher levels of nested hierarchies also occupy larger spatial scales. Thus, levels of organization in a nested hierarchical system can be ordered according to their relative position in a coordinate space defined by time and space scales (Figure 1). This coincidence, between level of organization and time and space scales, is an important theme in considerations of ecological hierarchies (Delcourt et al. 1983, Urban et al. 1987, Delcourt and Delcourt 1988, Carpenter 1989, King et al. 1990). Oceanographers (and limnologists?) have historically used a comparable structure to order their considerations of system variability (e.g., Stommel diagrams [Stommel 1963], Monin et al. 1977). Atmospheric scientists and geographers have adopted a similar approach (Dickinson 1988, Meentemeyer 1989).

The time and space scales of hierarchical organization represent scales of interaction (Allen and Starr 1982). The distribution of interaction frequency and strength define component subsystems or holons within the whole system. Discontinuities in the interactions define subsystem (holon) boundaries (Allen and Starr 1982). Rapid or frequent interactions occur within holons. Slower rates occur between holons. For example, in social mammals, interactions among family members are stronger and more frequent than interactions with other members of the local society, and interactions among the troop or band are more frequent than interactions between bands.

When interactions are dominated by physical characteristics of the ecosystem, scales of interaction, subsystem (holon) boundaries, may be obvious. In the terminology of Allen and Starr (1982) or O'Neill et al. (1986), the holon (subsystem) becomes tangible. For example, the spatial extents and water retention times of a topographically defined watershed represents a "natural" scale in the system bound together by the flow of water (e.g., the cycling of a water soluble nutrient). The time and space scales of the watershed delineate a specific, well defined, tangible subsystem. Interactions among subsystems at this scale, for example, the combination of first-order watersheds to form second-order watersheds, produce the next higher-level subsystem with its on natural scale. Physical processes of turbulent mixing in oceans and larger lakes can similarly impress natural scales on system interactions (e.g., the concentrations of phytoplankton growth and subsequent trophic interactions in eddies and gyres). The physical limitation set by the penetration of light (the euphotic zone) is another example. However, the phenomenon of "natural" scales applies equally to less physically bound subsystems. For example, in the system defined by competitive interactions among trees in a mesic forest, Urban et al. (1987) recognize scales of germination, tree replacement, suc-
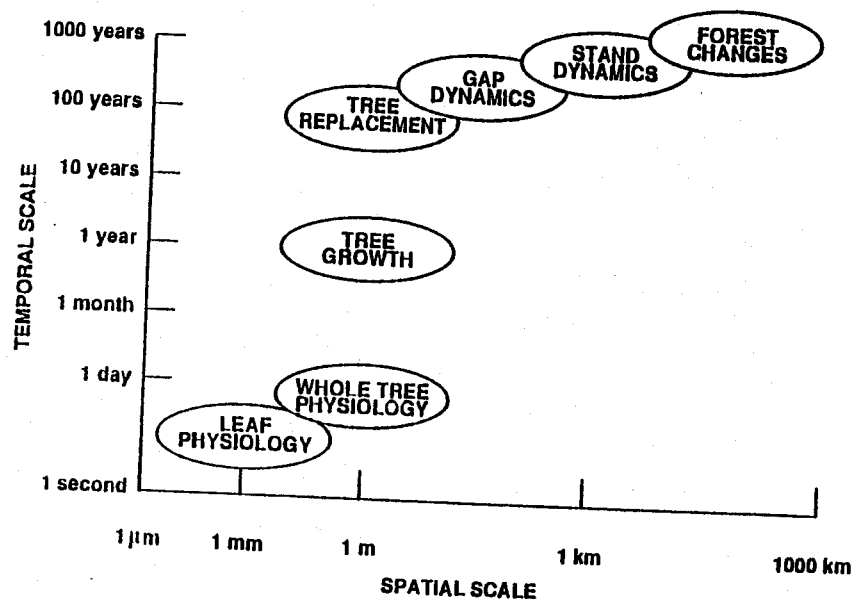
Figure 1. An example of the ordering of hierarchically organized rate dynamics by their associated spatial and temporal scales. The ellipses represent levels of carbon-biomass dynamics in a forested ecosystem. From King *et al.* (1990).

cession, species migration, and species extinction, in order of increasing spatial extent. Similarly, trophic interactions among wolves and moose define natural scales in that system. For example, the foraging area utilized by a wolf pack and the time required to cover that area define a scale for the individual pack. Interactions among wolf packs generate a next level of larger scale defined by the spatial and temporal distribution of the packs' foraging areas. In systems defined by human interactions with nonhuman components, natural scales may be defined by such things as areas of resource harvest or roadside vistas (e.g., how frequently humans see, interact with, different parts of a park).

In some cases, interactions may impress physical, observable patterns in space and time. For example, the scale of gap-phase dynamics (interactions among individual trees) may be evident in the spatial distribution of tree species and stand structure (Urban *et al.* 1987). The activity of a beaver colony can impress distinct patterns on the landscape at scales determined by foraging behaviour and social interactions (Johnston and Naiman 1987). These physical patterns or structures may reinforce the responsible interactions or influence interactions of other system components, even when viewed from alternative perspectives. Consider the impact beaver ponds or wallows created by alligators, buffalo, or other large animals can have on the distribution and interaction of other species, nutrient cycling, and energy flow.

Interactions that occur within a level are symmetric. The holons within a level operate at similar rates and can mutually affect the behaviour of others. Relations, interactions, between levels are asymmetric. O'Neill *et al.* (1986) identify these asymmetric relationships as *constraints* (O'Neill *et al.* 1989). *Constraint* is a very general term, simultaneously useful and potentially confusing. A molecule of gas may be constrained both by the walls of a container and by interactions with neighboring molecules. Here, I limit my use of *constraint* to those controls that emerge as a consequence of system interactions. Other extra-system controls (e.g., the walls of the container) I refer to as boundary conditions.

Constraints from lower levels appear as *potentials* (the biotic potentials of O'Neill *et al.* [1989]. Behavior of a system at one level is partially a consequence of the aggregate, integrated, behaviour of lower level components. These lower level behaviours can set limits on the behaviour of higher levels. They are particularly evident as rate-limiting interactions (analogous to rate-limiting steps in chemical dynamics). For example, a higher level cannot process material at a rate faster than the fastest rate of its functional components responsible for that processing. Salthe (1985) refers to these lower-level limitations as initiating conditions.

Within a hierarchical system, potentials are normally not realized. Interactions among system components at a given level constrain the

expression of a behaviour to be less than the potential provided by lower levels. Again, with reference to rates, the behaviour will be slower than the potential. As noted above, it is this difference in rates that defines the levels of the hierarchy. The interactions at one level generate the components of the next higher level, forming the potential for those higher level components. The aggregate behaviour of components at one level is a property of the next higher level and appear to the individual components of a given level as part of their environment. O'Neill *et al.* (1989) thus identify constraints from higher levels as *environmental limits*. These limits may arise from the immediately higher level, as a consequence of symmetric interactions with components of similar rates, or they may arise from higher levels. The further removed, the slower the rates, the more likely they are to appear as part of a very slowly changing or constant environment. At a given level, a single component acting alone has little influence on the aggregate behaviour of the next higher level of which it is a part. However, it may be strongly constrained by that aggregate.

Consider a couple of simple examples. While it is true that a wildebeest herd migrates as a consequence of the movement of individuals, any single individual has very little influence on the stampeding behaviour of the migrating herd. The individual wildebeest is, however, strongly constrained to follow the herd, to "go with the flow." More subtly perhaps, a canopy is made up of individual leaves and canopy photosynthesis is a consequence of the photosynthesis of individual leaves. At the same time, the canopy is the environment of any individual leaf, and single leaf photosynthesis is constrained by this environment. Realized canopy photosynthesis is less than the sum of potential individual leaf photosynthesis.

The asymmetry of interaction in the vertical structure of a hierarchical system has important consequences for system integrity and response to perturbation. Signals or fluctuations from lower levels are attenuated, damped, by successively higher levels. The further removed the lower level is from the level being observed, the more complete the attenuation. The responses of higher levels are integrated, averaged, responses of lower levels. Thus, a detectable response of a higher level to perturbation, fluctuation, in a lower level requires either very strong change in one or a few lower level components or very extensive change in most or all of the lower level components. The change must perceptibly alter the average of the lower level components. This property of normal hierarchical structure isolates higher level organization from all but the most extreme or extensive lower level fluctuation or perturbation. When the higher levels begin to respond at frequencies very close to that of the lower levels, the hierarchical structure of the system has degraded. Whole system integrity is thus maintained by the asymmetric between-level relationships (or loose vertical coupling [Simon 1973]) of hierarchically organized systems.

Because system components at lower levels are constrained by the higher levels, changes or perturbations at higher levels frequently impact lower level components. Perturb a higher level and its component lower levels are largely constrained to follow. The reverse is not true. Most lower level perturbations will be attenuated. Consider again the wildebeest. Disruption of the wildebeests' annual migration route, an effort requiring large scale intervention, has an affect on every member of the herd. Removal of one individual, even a few, will have little or no consequence for the herd's behaviour. If we remove enough individuals, the herding behaviour or constraint is diminished by a diminution of interactions among individuals. The aggregate begins to act less-and-less like a herd, eventually collapsing into erratic individual behaviours. This loss of higher level organization will have dire consequences for the individual wildebeest dependent upon the context of the herd, and it can impact other components of the Serengeti ecosystem that are dependent upon the wildebeests' annual migration.

The relationship between scale and hierarchical level and the asymmetric relationship between levels suggest an expected relationship between the scale of perturbation and whole-ecosystem integrity. Local, fine scale, or short term perturbations are likely to be attenuated as they are transferred through paths of interaction to larger, longer term, coarser scales. The consequences of fine scale perturbations are seen in the integrated averaged behaviour at larger scales. This average will attenuate or mask all but the most extreme or extensive smaller scale perturbations. The greater the difference is between the scale of perturbation and the scale of observation for ecosystem integrity, the greater the degree of attenuation. This theoretical consideration reinforces the common sense expectation that localized short term perturbations are unlikely to have consequences for large ecosystems and long periods of time. When they do, chaotic behaviour (e.g., extreme sensitivity to initial conditions) or catastrophic behaviour (e.g., bifurcation) is an indication that: (a) the system is not organized as a nested, rate-ordered hierarchy, (b) the hierarchical structure has deteriorated, or (c) the system is in transition between alternative hierarchical organizations (O'Neill *et al.* 1989). In these circumstances, hierarchy theory will be of limited use in the analysis of ecosystem integrity.

Scale, Hierarchy, and Measures of Ecosystem Integrity

Ecosystem integrity is a holistic, whole-system property. It applies to the entire integrated system and not just one or more of its components. Core body temperature is similarly a holistic measure of thermal state in

homeotherms, and a crude analogy can be drawn between measures of body temperature and measures of ecosystem integrity. However, most ecosystems at issue extend over large areas and persist for long periods of time. It is thus difficult to devise large scale, single-valued measurements of ecosystem integrity comparable to using a thermometer to measure body temperature. Whatever empirical measurements we ultimately employ to characterize ecosystem integrity, these measurements will almost invariably come from scales and levels of organization smaller, finer, or lower than the entire system. Remote sensing holds the promise of larger-scale ecosystem measurements, but effective use of these measurements will require the determination of meaningful relationships between spectral signatures and other ecosystem attributes reflecting ecosystem integrity. In the interim, and to complement these efforts, we must normally deal with a set of measurements from scales smaller than the whole system. From this set of measurements, we must devise some collective integrated measure for the aggregate system.

The scaled interactions of a hierarchically organized ecosystem can act as natural integrators of local processes. This natural integration is especially evident in scales defined by physical characteristics of the system. Watersheds are a good example. Water flowing through the watershed integrates many local changes over a rather clearly defined extent. Similarly, the foraging of a wolf pack integrates the finer scale temporal and spatial variability of their prey.

Advantage can be made of these natural scales of integration. Focusing a field measurement campaign on these natural integrators can reduce the number of local measurements required to characterize the entire system. Measuring output at the point of watershed discharge provides an integrated, holistic, measure for the entire system over the spatial extent of the watershed. Only a single point measurement at the weir is needed to characterize the entire spatial extent of the watershed. The weir measurement also integrates temporal variations over the period of the watersheds retention time. Successive measures at the weir over time provide for further integration. Thus, if I could identify a single watershed containing the entire ecosystem of interest, I would be tempted to focus my measurements there, at the point of discharge. In a sense, I can "take the temperature of the watershed." Airsheds and bodies of water with periodic turnover are related examples of natural physical integrators. Additional examples of a slightly different nature include tree rings, which integrate small scale variability in small scale individual leaf photosynthesis (O'Neill et al. 1986), and top level consumers, which frequently integrate toxic contamination of the ecosystem through the process of bioaccumulation.

There are also disadvantages in using these natural integrators. Because they integrate a diversity of natural and anthropogenic variations, it may be difficult to ascribe cause and effect to observed changes. Annual wood production and stream nutrient concentration are each influenced by many factors. Isolating a single cause (e.g., an anthropogenic disturbance) can be difficult. Witness the difficulty of assigning cause to observations of forest dieback at higher altitudes of the eastern United States. Observed mortality could be a consequence of acid precipitation, but forest growth (or lack of it) integrates so many other factors (including natural succession) that it is difficult to precisely define the contribution of any one factor.

Larger scale, natural integrators also tend to attenuate or smooth out finer scale variability. This attenuation tends to remove fine scale noise from observations and it makes detection of significant signal or trend at larger scales more likely. However, it also filters out finer scale signals that may be indicative of developing problems. We are caught in the dilemma of making observations at the appropriate larger scales of the system, but with the nagging concern that we may be missing significant signals from finer-scales and limiting our ability to ascribe cause-and-effect to our observations. In compromise, larger scale measurements, taking advantage of natural integrators, may need to be complemented with finer scale measurements.

Despite their disadvantages, natural scales of integration, if they can be identified, should be utilized in the sampling design for measures of ecosystem integrity. Given the practical limitations on making field measurements over extensive areas and for long periods of time, it must surely be appropriate to structure the sampling design for most efficient returns. When the system is characterized by natural scales of interaction or integration, this means sampling with respect to those scales. For example, an ecosystem will normally exist across a range of time and space scales. Once the time-space boundaries of the ecosystem are identified, either by consideration of process or the boundaries of management units, it is essential that the observations used to characterize ecosystem integrity characterize the entire extent of the ecosystem. Finer scale heterogeneity is one of the factors determining the nature of this sample. If, for example, the ecosystem were the same over the entire extent (both in time and space) with respect to the observations for ecosystem integrity, only a single, smaller scale measurement would be necessary to represent the entire extent. As the heterogeneity of the system increases, a larger sample of finer grain is required to effectively characterize the entire ecosystem. Targeting scales of integration as close to the scale of the entire ecosystem as possible will reduce the number of samples necessary to meet that requirement. For example, fewer second order watersheds must be sam-

pled than first order watersheds to characterize a landscape. The identification of natural scales of integration may be used to locate holistic integrated measures like those at watershed weirs, or the scales may be used to stratify multiple, disaggregated, finer scale samples. These approaches might also be combined. Again using the watersheds as an example, a sampling strategy might take advantage of the scale structure of an ecosystem by including integrated measures at the weirs of ith-order watersheds (e.g., stream water chemistry) and supplementing these measurements with samples of soil columns spatially distributed within one or more of the ith-order watersheds. The distribution of samples within these watersheds would logically be stratified by watersheds of the ith-1 order. Similarly, holistic, integrated measures of the quality of wolf habitat in a wolf-moose ecosystem might be obtained by monitoring the fecundity and survivorship of all wolf packs within the extent of the ecosystem. Finer scale measurements of individual wolf health, prey density, and vegetation could be made within the home range of one or more of the packs.

Targeting scales close to the scale of the entire ecosystem of interest will also increase the likelihood that observed changes will be of consequence for the entire ecosystem. Changes in the soil chemistry of a few local sites are unlikely to be indications of changes in the chemistry of the entire ecosystem. Changes in the stream chemistry of higher order streams, on the other hand, are very likely an indication of a change in the entire ecosystem. Similarly, illness of a few wolves or local fluctuations in prey density will not likely be expressed as a change in the wolf population of the entire ecosystem. A decrease in reproductive output of even one pack is more likely to indicate a decline in the ability of the ecosystem to support wolves. Again, these larger scale integrated measures are invaluable in detecting change like a loss of ecosystem integrity, but they may have to be supplemented with finer scale measurements to determine cause and effect.

Natural scales of integration may be identified by considering the interactions that bind a system together and the medium of that interaction (e.g., nutrients and water flow or trophic interactions and the area traversed in foraging). Tangible physical attributes of the system may clearly demarcate scales of the system (e.g., watershed topography, windthrow areas, or lake shores and other physical barriers to movement). Quantitative analysis of spatial (or temporal) patterns may reveal less obvious scaled structure that can also be associated with hierarchical system dynamics (O'Neill et al. 1991). Allen and Starr (1982) discuss, at some length, methods of multivariate analysis of spatial and temporal time series data for identifying scale in community ecology. Turner et al. (1991) review the use of spatial statistics to identify scales in landscapes.

All of these methods and more may be utilized in identifying scales of integration in ecosystems. Decisions on which data to collect will primarily be influenced by the choice of indicators of ecosystem integrity (Rapport et al. 1985) which are, in turn, largely determined by the perspective used in defining the ecosystem. Allen and Starr (1982) note, with respect to the problem of deciding which data to collect and dealing with the bias of a priori perspective, that "The best we can do is to record as much as possible, as frequently as possible, for as long as possible, and hope that we have not innocently passed over crucial keys to understanding a system's behaviour." I believe this admittedly somewhat unsatisfying guideline applies to measures of ecosystem integrity. Allen and Starr (1982) go on to suggest that once the data are collected, data transformations and tools of data analysis are used to "illuminate the structure inherent in the data." Identification of scales of integration or hierarchical organization and other considerations of scale and hierarchy largely follow the choice of measures of ecosystem integrity, i.e., the perspective from which, or for which, integrity is being addressed.

It should be noted that the scales identified by any of the various analytical methods are as dependent upon the perspective or criteria used to order observations as are the chosen measures of ecosystem integrity. Furthermore, the scales of integration defined from one system perspective for one indicator may not coincide with those for another. For example, the scale of the ith order watershed subsystem in the system defined by waterflow may have little in common with the scale of the community or population bound together by competitive interactions or the dispersal of airborne propagules unfettered by local topography.

Because of the dependency of scales of integration on system definition, efforts should be made to identify the natural scale of the ecosystem from a variety of perspectives. This should at least be done for every perspective involved in the suite of indicators for ecosystem integrity. When natural scales of integration from different perspectives coincide, special attention can be given to measuring at those scales. These scales also tend to coincide with tangibles (e.g., watersheds) and they form natural targets for measuring or monitoring strategies. If, for example, a variety of perspectives converge on the scale of the ith order watersheds in an ecosystem, measurements for ecosystem integrity can be targeted towards these watersheds. Preservation of the integrity of these watershed subsystems may be crucial to the preservation of integrity for the entire ecosystem viewed from a variety of perspectives.

REFERENCES

Allen, T.F.H. and T.B. Starr. 1982. *Hierarchy: Perspectives for Ecological Complexity*. The University of Chicago Press, Chicago.

Allen, T.F.H., and T.W. Hoekstra. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. *J. Vegetation Science*. 1:5-12.

Allen, T.F.H., R.V. O'Neill, and T.W. Hoekstra. 1984. Interlevel relations in ecological research and management: some working principles from hierarchy theory. USDA Forest Service General Technical Report RM-110, 11 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Botkin, D.B., J.F. Janak, and J.R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60:849-873.

Carpenter, S.R. 1989. Temporal variance in lake communities: blue-green algae and the trophic cascade. *Landscape Ecology*. 3:175-184.

Clark, J.S. 1990. Integration of ecological levels: individual plant growth, population mortality, and ecosystem processes. *J. of Ecology*. 78:275-299.

Dickinson, R.E. 1988. Atmospheric systems and global change. In: T. Rosswall, R. G. Woodmansee, and P. G. Risser (eds.), *Scales and Global Change*. SCOPE 35. John Wiley and Sons, Chichester, England.

Delcourt, H.R., P.A. Delcourt, and T. Webb III. 1983. Dynamic plant ecology: the spectrum of vegetation change in space and time. *Quat. Sci. Rev.* 1:153-175.

Delcourt, H.R., and P.A. Delcourt. 1988. Quaternary landscape ecology: Relevant scales in space and time. *Landscape Ecology*. 2:23-44.

Evans, F. C. 1956. Ecosystems as the basic unit in ecology. *Science*. 123:1127-1128.

Foster, M.M., P.M. Vitousek, P.A. Randolph. 1980. The effect of *Ambrosia artemisiifolia* on nutrient cycling in a first-year old-field. *Am. Midl. Natur.* 103:106-113.

Golley, F.B. 1983. Introduction. pp. 1-8. In: F.B. Golley (ed.), *Tropical Rain Forest Ecosystems: Structure and Function*. Ecosystems of the World 14A. Elsevier Scientific Publishing Company, Amsterdam.

Harcombe, P.A. 1977. Nutrient accumulation by vegetation during the first year of recovery of a tropical forest ecosystem. pp. 437-378. In: J. Cairns, Jr., K. L. Dickson, and E. E. Herricks (eds.), *Recovery and Restoration of Damaged Ecosystems*. University Press of Virginia, Charlottesville.

Howell, F.G., J.B. Gentry, and M.H. Smith (eds.). 1975. *Mineral Cycling in Southeastern Ecosystems*. ERDA Symposium Series. U.S. Energy Research and Development Administration. CONF-740513. Available from National Technical Information Center, U.S. Department of Commerce, Springfield, Virginia.

Huston, M., D.L. DeAngelis, and W.M. Post. 1988. New computer models unify ecological theory. *BioScience*. 38:682-691.

Johnston, C.A., and R.J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. *Landscape Ecology*. 1:47-57.

King, A.W., W.R. Emanuel, and R.V. O'Neill. 1990. Linking mechanistic models of tree physiology with models of forest dynamics: problems of temporal scale. pp. 241-248. In: *Process Modeling of Forest Growth Responses to Environmental Stress*. edited by R. K. Dixon, R. S. Meldahl, G. A. Ruark, and W. G. Warren. Timber Press, Portland, Oregon.

Krebs, C.J. 1978. *Ecology: The Experimental Analysis of Distribution and Abundance*. 2nd Ed. Harper and Row, New York.

Limburg, K.E., M.A. Moran, and W.H. McDowell. 1986. *The Hudson River Ecosystem*. Springer-Verlag, New York.

Lindeman, R.L. 1942. The trophic dynamic aspect of ecology. *Ecology*. 23:399-418.

Magnuson, J.J., H.A. Regier, W.J. Christie, and W.C. Sonzogni. 1980. To rehabilitate and restore Great Lakes ecosystems. pp. 95-112. In: J. Cairns, Jr. (ed.), *The Recovery Process in Damaged Ecosystems*. Ann Arbor Science, Ann Arbor, Michigan.

McCormick, J.F., and R.B. Platt. 1980. Recovery of an Appalachian forest following the chestnut blight or Catherine Keever—you were right. *Am. Midl. Natur.* 104:264-273.

McNaughton, S.J., and L.L. Wolf. 1979. *General Ecology*. Second Edition. Holt, Rinehart, and Winston, New York.

Meentemeyer, V. 1989. Geographical perspectives of space, time, and scale. *Landscape Ecology*. 3:163-175.

Monin, A.S., V.M. Kamenkovich, V.G. Kort. 1977. *Variability of the Oceans*. John Wiley and Sons, New York.

Odum, E.P. 1971. *Fundamentals of Ecology*. 3rd Edition. Saunders, Philadelphia.

Odum, H. T. 1983. *Systems Ecology: An Introduction*. John Wiley and Sons, New York.

O'Neill, R.V., B.S. Ausmus, D.R. Jackson, R.I. Van Hook, P. Van Voris, C. Washburne, and A.P. Watson. 1977. Monitoring terrestrial ecosystems by analysis of nutrient export. *Water Air Soil Pollut.* 8:271-277.

O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton, New Jersey.

O'Neill, R.V., A.R. Johnson, and A.W. King. 1989. A hierarchical framework for the analysis of scale. *Landscape Ecology*. 3:193-205.

Overton, W.S. 1972. Toward a general model structure for forest ecosystems. In: J.F. Franklin (ed.), *Proc. Symp. on Research on Coniferous Forest Ecosystems*. Northwest Forest Range Station, Portland.

Overton, W.S. 1975. The ecosystem modeling approach in the coniferous forest biome. pp. 117-138. In: B. C. Patten (ed.), *Systems Analysis and Simulation in Ecology*. Vol. III. Academic Press, New York.

Paine, R.T. 1966. Food web complexity and species diversity. *Am. Nat.* 100:65-75.

Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry.* 2:3-27.

Pastor, J., and W.M. Post. 1988. Response of northern forests to CO_2-induced climatic change: dependence on soil water and nitrogen availabilities. *Nature.* 34:55-58.

Patten, B.C. 1982. Environs: relativistic elementary particles for ecology. *American Naturalist.* 119:179-219.

Post, W. M., and J. Pastor. 1990. An individual-based forest ecosystem model for projecting forest response to nutrient cycling and climate changes. pp. 61-74. In: L. C. Wensel and G. S. Biging (eds.), *Forest Simulation Systems*. University of California.

Rapport, D.J., H.A. Regier, and T.C. Hutchinson. 1985. Ecosystem behaviour under stress. *American Naturalist.* 125:617-640.

Reichle, D.E. 1981. *Dynamic Properties of Forest Ecosystems*. Cambridge University Press, Cambridge, United Kingdom.

Rosen, R. 1977. Observation and biological systems. *Bulletin of Mathematical Biology.* 39:663-678.

Ruark, G.A., and J.G. Bockheim. 1988. Biomass, net primary production, and nutrient distribution for an age sequence of *Populus tremuloides* ecosystems. *Can. J. For. Res.* 18:435-443.

Rykiel, E.J., Jr., and N.T. Kuenzel. 1971. Analog computer models of "The Wolves of Isle Royale". pp. 513-541. In: B. C. Patten (ed.), *Systems Analysis and Simulation in Ecology*. Vol. 1. Academic Press, New York.

Salthe, S.N. 1985. *Evolving hierarchical systems: their structure and representation*. Columbia University Press, New York.

Shilov, I.A. 1981. The biosphere, levels of organization of life, and problems of ecology. *Soviet J. Ecol.* 12:1-6.

Shugart, H.H. 1984. *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models.* Springer-Verlag, New York.

Shugart, H.H., Jr., and D.C. West. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *J. Environ. Management.* 5:161-179.

Simon, H.A. 1973. The organization of complex systems. pp. 3-27. In: H.H. Pattee (ed.), *Hierarchy Theory.* Braziller, New York.

Sinclair, A.R.E., and M. Norton-Griffiths. 1979. *Serengeti: Dynamics of an Ecosystem.* University of Chicago Press, Chicago.

Stommel, H. 1963. Some thoughts about planning the Kuroshio survey. pp. 22-23. In: *Proceedings of Symposium on the Kuroshio, Tokyo.*

Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. *Ecology.* 16:284-307.

Turner, M.G., and R.H. Gardner. 1991. Quantitative methods in landscape ecology: an introduction. pp. 3-14. In: M.G. Turner and R.H. Gardner (eds.), *Quantitative Methods in Landscape Ecology.* Springer-Verlag, New York.

Urban, D.L., R.V. O'Neill, and H.H. Shugart, Jr. 1987. Landscape ecology. *Bioscience.* 37:119-27.

Vitousek, P.M. 1986. Biological invasions and ecosystem properties: can species make a difference? pp. 163-176. In: H. A. Mooney and J.A. Drake (ed.), *Ecology of Biological Invasions of North America and Hawaii.* Springer-Verlag, New York.

Vogl, R.J. 1980. The ecological factors that promote perturbation-dependent ecosystems. pp. 63-94. In: J. Cairns, Jr. (ed.), *The Recovery Process In Damaged Ecosystems.* Ann Arbor Science, Ann Arbor, Michigan.

Walters, C.J. 1971. Systems ecology: the systems approach and mathematical models in ecology. pp. 276-292. In: E.P. Odum, *Fundamentals of Ecology.* 3rd. Ed. W. B. Saunders, Philadelphia.

Webster, J.R. 1979. Hierarchical organization of ecosystems. In: *Theoretical Systems Ecology.* ed. E. Halfon, pp. 119-31. New York: Academic Press.

Williams, R.B. 1971. Computer simulation of energy flow in Cedar Bog Lake, Minnesota based on the classical studies of Lindeman. pp. 543-582. In: B.C. Patten (ed.), *Systems Analysis and Simulation in Ecology.* Vol. 1. Academic Press, New York.

Zak, D.R., and K.S. Pregitzer. 1990. Spatial and temporal variability of nitrogen cycling in northern Lower Michigan. *Forest Science.* 36:367-380.