

Hierarchy and Scaling: Extrapolating Information Along a Scaling Ladder

by J. Wu

RÉSUMÉ

La complexité des systèmes écologiques est due à la combinaison du grand nombre de composantes, des interactions non-linéaires entre elles, de délais temporels ainsi que de phénomènes de rétroaction et de l'hétérogénéité spatiale. Afin de comprendre les systèmes écologiques et comment on peut passer d'une échelle d'observation à une autre, on se doit de tenir compte de cette complexité. La théorie de la hiérarchie suggère que les systèmes écologiques sont en fait des systèmes presque décomposables à cause du couplage vertical et horizontal non serré de leur structure et de leur fonctionnement. Ces systèmes peuvent donc être simplifiés en se basant sur les principes de décomposition spatio-temporelle. Le concept unificateur de plusieurs disciplines en sciences de la terre, celui de la dynamique des parcelles, est une des meilleures approches pour tenir compte efficacement de l'hétérogénéité spatiale. L'intégration de la théorie de la hiérarchie et du concept de la dynamique des parcelles a mené à l'émergence du paradigme de la dynamique des parcelles hiérarchiques. Dans cet article, je discute des notions qui se rattachent à la complexité écologique, de la théorie de la hiérarchie et de la dynamique des parcelles hiérarchiques, puis je présente une stratégie hiérarchique de changement d'échelles. Cette stratégie comporte trois étapes: (1) identifier les parcelles hiérarchiques appropriées, (2) faire des observations et développer des modèles des structures et des processus autour des niveaux choisis, et (3) extrapoler d'une échelle d'observation à l'autre en employant des modèles hiérarchiques. Identifier et prendre en compte la structure hiérarchique, ainsi que la quasi-décomposition des systèmes écologiques complexes, sont essentiels à la compréhension et la prédiction en écologie, car l'approche hiérarchique facilite grandement la simplification des systèmes et le passage de l'information d'une échelle d'observation à une autre. Il est difficile à justifier théoriquement et très difficile techniquement de traduire l'information directement entre les deux niveaux distants, lorsque l'on ignore les autres niveaux pertinents au phénomène étudié. Malgré qu'il soit possible de passer de la cellule au globe, et vice-versa, pour que cette démarche soit valable, elle se doit d'être hiérarchique. Le présent article décrit une telle approche, soit celle de parcelles hiérarchiques, qui est employée comme "échelle de changements

d'échelles d'observation". Cette approche peut aider à simplifier la complexité des systèmes étudiés et par le fait même aider à la compréhension écologique, tout en minimisant le danger de propagation d'erreurs lors du passage de l'information d'une échelle d'observation à une autre.

SUMMARY

The large number of components, nonlinear interactions, time delays and feedbacks, and spatial heterogeneity together often make ecological systems overwhelmingly complex. This complexity must be effectively dealt with for understanding and scaling. Hierarchy theory suggests that ecological systems are nearly completely decomposable (or nearly decomposable) systems because of their loose vertical and horizontal coupling in structure and function. Such systems can thus be simplified based on the principle of time-space decomposition. Patch dynamics provide a powerful way of dealing explicitly with spatial heterogeneity, and have emerged as a unifying concept across different fields of earth sciences. The integration between hierarchy theory and patch dynamics has led to the emergence of the hierarchical patch dynamics paradigm (HPDP). In this paper, I shall discuss some major elements of ecological complexity, hierarchy theory, and hierarchical patch dynamics, and then present a hierarchical scaling strategy. The strategy consists of three stages, each of which may involve a number of steps and methods: (1) identifying appropriate patch hierarchies, (2) making observations and developing models of patterns and processes around focal levels, and (3) extrapolation across the domains of scale using a hierarchy of models. Identifying and taking advantage of the hierarchical structure and near-decomposability of complex ecological systems are essential to understanding and prediction because a hierarchical approach can greatly facilitate simplification and scaling. It is hardly justifiable

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theoretically and overwhelmingly difficult technically to translate information directly between two distant levels (or corresponding scales), when ignoring intervening levels that are relevant to the phenomenon under study. Although it may be possible to scale up from the cell to globe, or vice versa, successful approaches most likely have to be hierarchical. In this paper, I shall describe one such approach in which patch hierarchies are used as "scaling ladders". This scaling ladder approach can help simplify the complexity of systems under study, enhance ecological understanding, and, at the same time, minimize the danger of intolerable error propagation in translating information across multiple scales.

Key Words: *Scale, scaling, hierarchy theory, hierarchical patch dynamics, grain, extent, aggregation, extrapolation, near-decomposability, space-time decomposition, pattern and process.*

"The world is both richly strange and deeply simple. That is the truth spelled out in the graininess of reality; that is the consequence of modularity. Neither gods nor men mold clay freely; rather they form bricks." (Philip Morrison, 1966)

INTRODUCTION

Traditionally, most empirical and theoretical studies in ecology have been conducted over small areas and short time periods and poorly replicated. For example, Kareiva and Anderson (1986) reported that 50% of ecological experiments published in the journal, *Ecology*, between 1980 and 1987 were conducted on plots less than 1m in diameter. In a similar survey, Tilman (1989) found that only 7% of experiments he examined were conducted on a time scale greater than five years, while 40% lasted less than 1 year (typically a single field season). Until now, only a few whole ecosystems have been subjected to experimental manipulation and are usually not replicable or controlled (Carpenter *et al.*, 1995). As a result, patterns and processes of ecological systems that occur on broad spatial (e.g., the human landscape and above) and temporal (e.g., decades and longer) scales are poorly understood. However, the recent literature in ecology and related fields of earth sciences clearly indicates an increasing emphasis on studies at coarse scales and over multiple scales. This shift in research emphasis in ecology seems inevitable for at least two reasons. The first is that most, if not all environmental and resource management problems, can only be dealt effectively with at broad scales on which they typically occur. The second and more profound reason is that ecologists are now acutely aware that, in order to understand how nature works, they must consider broad-scale patterns and process and relate them to those at fine scales which are most familiar to them. In both cases, translating or extrapolating information from one scale to another, i.e., scaling, is indispensable. Accordingly, the process of translating or extrapolating information from fine to coarse scales is usually referred to as scaling-up, and the process in the reverse direction

as scaling-down. Clearly, there is an urgent need to conduct large-scale studies for capturing the patterns and processes that are not evident in fine-scale observations, and to develop strategies for translating information from local to regional and global scales. Indeed, the issues of scale and scaling have taken a prominent position in ecology (Levin, 1992; Peterson and Parker, 1998). Not surprisingly, these recent studies have shown that scaling is usually complex, with problems and obstacles arising from a variety of situations.

Why is scaling a complex matter? First, studies in landscape ecology, hydrology, meteorology, and other related earth sciences have shown that different controls and processes tend to dominate in distinctive, characteristic domains of scale in time and space. Thus, observations made on a single scale can, at best, capture only those patterns and processes pertinent to that scale of observation. Yet, complexity arises almost inevitably when a description or explanation simultaneously invokes multiple levels of organization or domains of scale (Simon, 1962; Allen and Starr, 1982). Second, nonlinear relationships and feedbacks among components at the same and different scales are quite common in ecological systems. Strong nonlinearities often lead to instability and unpredictability in large complex systems. Third, spatial heterogeneity is ubiquitous and varies at different scales, further complicating the scaling process. For example, while landscapes can be perceived as hierarchical mosaics of patches, at each level patches may interact in a variety of ways and form different patterns. Patchiness and gradients usually interweave and result in spatial or structural nonlinearity in landscapes. Thus, patch dynamics within a landscape usually are complex, due to the functional and spatial nonlinearities. These scale-dependent processes and nonlinearities explain why emergent properties are frequently encountered when we move across organizational levels and spatio-temporal scales. Thus, a successful scaling strategy must be able to effectively tackle these complex aspects of ecological systems. While the issue of scaling has been widely recognized as essential in both basic and applied research, a general theory of scaling is still elusive.

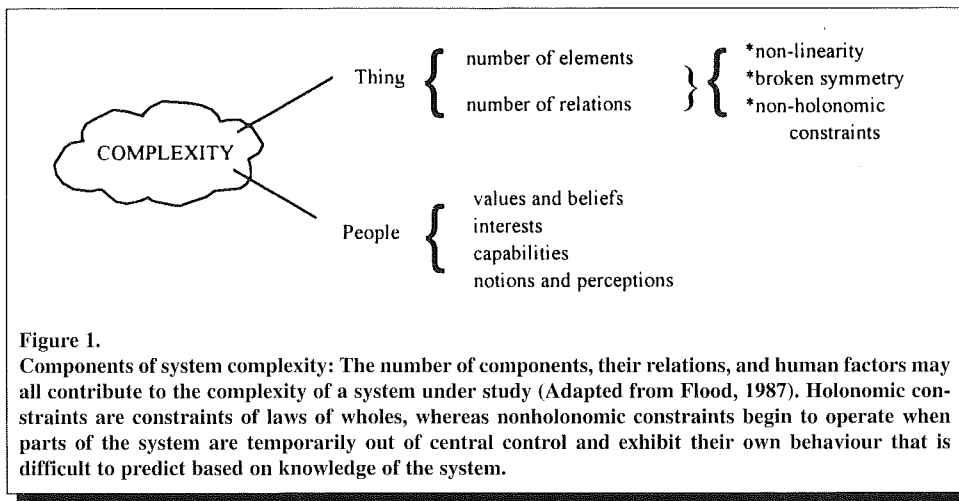
Given that ecological systems comprise multi-leveled or multi-scaled patterns and processes, are there general rules for scaling up or down? How do the number of scales (or hierarchical levels), nonlinearity, and patchiness affect the feasibility and accuracy of scaling? How much detail needs to be incorporated (or discarded) for a given scaling purpose? Is it possible or necessary to scale from the cell up to the biosphere? More to the point, how? The main purpose of this paper is, therefore, to address some of these questions by presenting a hierarchical patch dynamics scaling strategy.

COMPLEXITY OF ECOLOGICAL SYSTEMS AND HIERARCHY THEORY

Complexity of Ecological Systems

Complexity of a system is usually related to the number of components, their relationships, and various factors associated with the observer. Although complex systems tend to have a

great number of components, it is the complex interactions among components that make them difficult to deal with. A comprehensive concept of complexity must include both inherent system properties and the perceptions, interests, and capabilities of the observer (**Figure 1**). The complexity of ecological systems, viewed from a scaling perspective, comprises the multiplicity of spatial patterns and ecological processes, nonlinear interactions among numerous components, and heterogeneity in space and time. Again, it is important to note that whether or not a particular ecological system is complex may depend on the way it is described and the objective of an investigation. For example, if one needs only to predict (rather than explain) how the productivity of a given ecosystem is related to precipitation in the growing season, a simple regression equation based on enough historical data often does an adequate job (at least over a short period of time). In this case, the observer basically sees the system as a "black box" and is interested primarily in the relationship between its input and output.



Weaver (1948) identified three ranges of complexity in terms of the properties of system structure: organized simplicity, organized complexity, and disorganized complexity, which correspond to Weinberg's (1975) small-number, middle-number, and large-number systems, respectively. Organized simplicity, characterizing systems which have a smaller number of significant components that interact deterministically, can be dealt with readily by analytical mathematics. A system involving many factors may always appear complex at the first glance, but it is not so if only a limited number of them are actually significant with respect to the question being addressed. Disorganized complexity occurs when a system has a large number of significant components that exhibit a high degree of random behaviour, and thus can be dealt with effectively by using statistical methods. However, most systems we have to deal with in ecology and environmental science are middle-number systems which are characterized by organized complexity (Allen and Starr, 1982; O'Neill *et al.*, 1986; Flood, 1987). On the one hand, these systems have more components than analytical mathematics can handle; on the other hand, the use of traditional statistical methods cannot

be justified because of the inadequate number, and non-random behaviour, of components. As a result, quantitative methods are lacking for effectively untangling organized complexity. Consequently, we must either somehow convert middle-number systems into small-number systems whenever possible, or develop new methods that differ fundamentally from the well-established mathematical and statistical procedures. Systems science was developed in particular to cope with these challenges (Weinberg, 1975; Flood and Carson, 1993). With its emphasis on processes and dynamics, systems approaches have been rather powerful and successful in dealing with complex feedbacks and nonlinear interactions in engineering, social, economic, and ecological systems, but they often become inadequate once spatial heterogeneity needs to be considered explicitly.

Simon (1996) identified three bursts of interest in complexity and complex systems in the 20th century. The first burst started after World War I, signified by the terms of "holism", "Gestalts", and "creative evolution", which had a strong anti-reductionist flavour. The second one, characterized by such terms as "general systems", "information", "cybernetics", and "feedback", began after World War II, and focused primarily on the roles of feedback and homeostasis in maintaining system stability. The current eruption has focused mainly on mechanisms that create and sustain complexity and on methods that can effectively describe and analyze complexity. As a result, alternative views on complexity have been emerging, which can be identified with terms "chaos", "catastrophe", "fractals", "cellular automata", "genetic algorithms", and "hierarchy". These views emphasize different aspects of complexity and can be perceived as both alternatives and complements to hierarchy theory (Simon, 1996). While all of them are useful for understanding cross-scale phenomena, I argue that hierarchy theory can provide a much needed conceptual framework for developing successful scaling theories and approaches.

Hierarchy Theory

Hierarchy theory emerged from the need for dealing with complexity in studies across a variety of disciplines, including management science, economics, psychology, biology, ecology, and systems science (Simon, 1962, 1973; Koestler, 1967; Whyte *et al.*, 1969; Mesarovic *et al.*, 1970; Weiss, 1971; Pattee, 1973; Miller, 1978; Allen and Starr, 1982; Salthe, 1985; O'Neill *et al.*, 1986; Ahl and Allen, 1996). A hierarchy can broadly be defined as "a partial ordering" of entities (Simon, 1973). In his seminal paper on the architecture of complexity, Simon (1962) most insightfully noted that complexity frequently takes the form of hierarchy, whereby a complex system consists of interrelated subsystems that are in turn composed of

their own subsystems, and so on, until the level of elementary or "primitive" components is reached. The choice of the lowest level in a given system is dependent not only on the nature of the system, but also on the research question.

In the literature of hierarchy theory, the subsystems that comprise a level are usually called "holons" (from the Greek word *holos* = whole and the suffix *on* = part or particle as in proton or neutron; coined by Koestler, 1967). The word holon has been widely adopted, mainly because it conveys the idea that subsystems at each level within a hierarchy are "Janus-faced": they act as "wholes" when facing downwards and as "parts" when facing upwards. It is important to note that the levels in the traditional hierarchy of ecological organization (i.e., individual-population-community-ecosystem-landscape-biome-biosphere) are definitional and do not necessarily meet scalar (i.e., scale-related, albeit spatial or temporal) criteria (see Allen and Hoekstra, 1992; Ahl and Allen, 1996; O'Neill and King, 1998). However, the concepts and principles of hierarchy theory usually apply only to scalar, not prescribed or definitional, hierarchies.

A hierarchical system has both vertical structure that is composed of levels and horizontal structure that consists of holons (Figure 2). Hierarchical levels are separated, fundamentally, by characteristically different process rates (e.g., behavioural frequencies, relaxation time, cycle time, or response time). The boundaries between levels and holons are termed surfaces (Allen and Starr, 1982), which in space are the places exhibiting the highest variability in the strength of interactions (Allen *et al.*, 1984). Surfaces filter the flows of matter, energy, and information crossing them, and thus can also be perceived as filters (Ahl and Allen, 1996). In hierarchical systems, higher levels are characterized by slower and larger entities (or low-frequency events) and for lower levels by faster and smaller entities (or high-frequency events). The relationship between two adjacent levels is asymmetric: the upper level exerts constraints (e.g., as boundary conditions) to the lower level, whereas the lower provides initiating conditions to the upper.

On the other hand, the relationship between subsystems (holons) at each level is symmetric, and can be distinguished by the degree of interactions among components. That is, components interact more strongly or more frequently within than between subsystems or surfaces. For example, the strength of interactions between subatomic components is stronger than that between atoms, which is in turn stronger than that between molecules. The same can be said about an ecological hierarchy such as the nested hierarchy of individual-local population-metapopulation or leaf-canopy-stand-landscape. Therefore, it is the variability in the strength of interactions between levels and among holons that defines the locations of surfaces, and it is the relatively high degree of interactions among components that gives rise to the apparent identity and integrity of holons as well as systems.

These characteristics of hierarchical structure can be explained by virtue of "loose vertical coupling", permitting the distinction between levels, and "loose horizontal coupling", allowing the separation between subsystems (holons) at each level (Simon, 1973). The existence of vertical and horizontal loose couplings is exactly the basis of the decomposability of complex systems (i.e., the feasibility of a system being disassembled into levels and holons without a significant loss of information). Decomposability and decomposition (i.e., the process of separating and ordering system components according to their temporal or spatial scales or both) represent one of the most essential tenets of hierarchy theory. While the word "loose" suggests "decomposable", the word "coupling" implies resistance to decomposition. Strictly speaking, complete decomposability only occurs when coupling between components becomes zero, which seems a trivial case because, by definition, a system is composed of interacting parts. Thus, hierarchical complex systems are only nearly completely decomposable or nearly decomposable (Simon, 1962, 1973).

The concept of near-decomposability can be defined precisely in mathematical terms for dynamic systems (Simon and Ando, 1961; Overton, 1975a). Ando and Fisher (1963) provided a mathematical definition as follows: "A completely decomposable matrix is a square matrix such that an identical rearrangement of rows and columns leaves a set of square sub-matrices on the principal diagonal and zeros everywhere else. ... A decomposable matrix (as opposed to a completely decomposable one) is a square matrix such that an identical rearrangement of rows and columns leaves a set of square sub-matrices on the principal diagonal with zeros everywhere below (but not necessarily also above such matrices). ... Near-decomposability and near-complete-decomposability are defined by replacing the zeros in the above definitions by small nonzero numbers." Both conceptually and mathematically, the problem of decomposition is closely related to the one of aggregation, for which various analytical methods have been developed for ecological systems (see Cale and

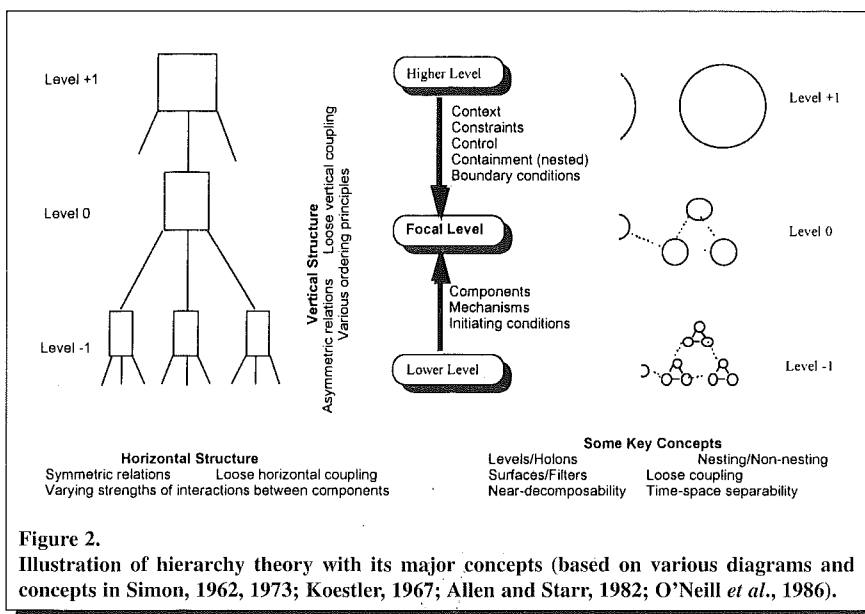


Figure 2. Illustration of hierarchy theory with its major concepts (based on various diagrams and concepts in Simon, 1962, 1973; Koestler, 1967; Allen and Starr, 1982; O'Neill *et al.*, 1986).

Odell, 1979; O'Neill and Rust, 1979; Schaffer, 1981; Gardner *et al.*, 1982; Iwasa *et al.*, 1987, 1989; Bartell *et al.*, 1988; Heuvelink *et al.*, 1989; King *et al.*, 1991; Rastetter *et al.*, 1992; Hiebeler, 1997).

According to the principle of decomposition, for a given study that is focused on a particular level, constraints from higher levels are expressed as constants or boundary conditions whereas the rapid dynamics at lower levels are filtered (smoothed out) and only manifest as averages or equilibrium values. One of the most important implications of decomposition is that the short-term dynamics of subsystems can be effectively and justifiably studied in isolation by ignoring the between-subsystem interactions that operate over significantly longer time scales. On the other hand, the long-term dynamics of the entire system is predominantly determined by the slow processes. The principle of near-decomposability has been demonstrated mathematically for both linear and nonlinear dynamic systems in economics (e.g., Simon and Ando, 1961; Ando and Fisher, 1963; Fisher, 1963) and ecology (e.g., Cale and Odell, 1979; O'Neill and Rust, 1979; Gardner *et al.*, 1982; Iwasa *et al.*, 1987, 1989; Bartell *et al.*, 1988). For a specific problem it is not only possible, but also wise to "scale off" (sensu Simon, 1973) relevant levels from those above and below, thus achieving a greater simplification and better understanding.

Therefore, it is the near-decomposability, as defined in hierarchy theory, that makes it possible to transform a middle-number system into a small-number system or, at least, to reduce the magnitude of complexity to a more manageable level. In other words, the nearly decomposable nature of complex systems provides a key to its simplification and manageability. For example, hydraulic and aerodynamic systems are full of turbulence and thus chaotic and unpredictable (or "unmanageable") in any detail, but they become "manageable" when they are dealt with as aggregate phenomena (Simon, 1996). The first-, second-, and third-order closure methods in micrometeorological models can be viewed as distinct ways of decomposing the complex vegetation-atmosphere system with increasing detail in representing turbulent flows (Paw U *et al.*, 1985; Wu, 1990). Although the degree of decomposability is more than likely to vary between systems or even between processes within the same system, near-decomposability appears to be rather common in nature (Whyte *et al.*, 1969; Weiss, 1971; Pattee, 1973; Courtois, 1985; Klir, 1985; Kolasa, 1989; Holling, 1992). Indeed, near-decomposability seems to underline the plausibility and success of seemingly independent and partial studies of nature crossing different hierarchical levels, ranging from elementary particles to the cosmos, and focusing on different phenomena ranging from physical to social sciences (Courtois, 1985). Apparently, the wisdom reflected in the statement, "Everything is connected to everything else", often encountered in ecological literature, is after all not helpful or even misleading for understanding complex systems or developing scaling theories. Evidently, for any given phenomenon in this world, some things are more connected than others, and most things are only negligibly interrelated with each other (Simon, 1973). However, we must also keep in mind that it is the weak inter-

actions that do, but only, affect the long-term system dynamics beyond the time frame that is tailored by the nature of particular phenomena and the objective of a study.

Hierarchy theory suggests that when one studies a phenomenon at a particular hierarchical level (the focal level, often denoted as Level 0), the mechanistic understanding comes from the next lower level (Level -1), whereas the significance of that phenomenon can only be revealed at the next higher level (Level +1). Interestingly, Baldocchi (1993) called the three adjacent scales the reductionist (Level -1), operational (Level 0), and macro (Level +1) scales, respectively. This three-level structure is sometimes referred to as the Triadic structure of hierarchy (O'Neill, 1989). Thus, three adjacent levels or scales usually are necessary and adequate for understanding most of the behaviour of ecological systems (O'Neill, 1988, 1989; Salthé, 1991) although occasional exceptions to this general rule may occur when certain effects penetrate through several levels above or below (so-called perturbing transivities by Salthé, 1991; see O'Neill *et al.*, 1991 for specific examples). Simon (1973) clearly stated: "The fact that nature is hierarchic does not mean that phenomena at several levels cannot, even in the Mendelian view, have common mechanisms. Relativistic quantum mechanics has had spectacular success in dealing with phenomena ranging all the way from the level of the atomic nucleus to the level of tertiary structure in organic molecules. ... Scientific knowledge is organized in levels, not because reduction in principle is impossible, but because nature is organized in levels, and the pattern at each level is most clearly discerned by abstracting from the detail of the levels far below."

How to derive the hierarchical structure of complex systems? Different ordering principles result in different hierarchies. It is perceivable that hierarchies with different structure and properties can be derived to describe the same system using alternative ordering criteria. Two types of hierarchies, in particular, should be recognized: nested and non-nested hierarchies (Allen and Starr, 1982; Ahl and Allen, 1996). Nested hierarchies are the special case in which the components (holons) of one level contain, or are composed of, the components (also holons) of the next level down (e.g., taxonomic or land cover classification systems). However, containment is not a part of the ordering criteria for non-nested hierarchies (e.g., hierarchies of trophic levels). Although both of them comply with the general concepts and principles of hierarchy theory, do behave differently, in several ways (see **Table 1**).

Why do complex systems like ecosystems possess hierarchical structures? The well-known parable of watchmakers (Simon, 1962) seems more than just heuristic (**Figure 3**). Two fine watchmakers arrived at two entirely different destinations only because of the difference in the watch-building strategy. The hierarchical or modular approach led one to success, whereas the extreme bottom-up, reductionistic approach led the other to failure (see **Figure 3** for more details). Therefore, Simon (1962) concluded that "hierarchies will evolve much more rapidly from elementary constituents than will non-hierarchical systems containing the same number of elements." For example, mathematical calculations based on known biological

Table 1.
Comparison between non-nested and nested hierarchies (based on discussions in Ahl and Allen, 1996).

Non-nested hierarchies	Nested hierarchies
Not suitable for exploration	Suitable for exploration
Same criteria (or measurement units) pressing across all levels	Different criteria (or measurement units) at different levels
Comparison between hierarchies is more feasible	Comparison between hierarchies is less feasible
System-level understanding cannot be obtained by knowledge of parts	System-level understanding can be obtained by knowledge of parts

facts and probability theory suggest that the level of complexity in today's biological world would not be possible to achieve through evolution if the biological complexity were not hierarchically structured (see Simon, 1962, 1973).

What implications does this parable have for understanding complexity, hierarchy, and scaling? It provides enlightening, although heuristic, insight into understanding the complexity of nature and the nature of complexity. Biological and ecological systems usually are hierarchically structured because such an architecture tends to evolve faster, allow for more stability, and thus is favoured by natural selection (Simon, 1962; Whyte *et al.*, 1969; Pattee, 1973; Salthe, 1985; O'Neill *et al.*, 1986). The parable also reminds us of many successful methods and approaches associated with the concept "modularity" from biology to computer sciences, which apparently is a derivative of hierarchy. Although not all hierarchical systems are stable, the construction of a complex system using a hierarchical approach is more likely to be successful than otherwise. For example, to build complex, yet stable and efficient software, computer scientists have developed the object-oriented paradigm, which in many ways reflects the principles of hierarchy theory (Booch, 1994). In general, successful human problem-solving procedures are hierarchical (Newell and Simon 1972). As discussed earlier in the context of decomposability, a very important utility of hierarchy theory is to simplify complexity. According to Miller (1956; cited in Simon, 1973), the maximum number of chunks of information an individual can simultaneously comprehend is on the order of seven, plus or minus two, while it takes the mind about five seconds to accept a new chunk of information. Thus, a non-hierarchical complex system can not be fully described, and even if it could, it would be incomprehensible.

From the above review, it becomes apparent that the major developments in hierarchy theory are relatively recent, although the concepts of "levels" of organization and "hierarchy" date back to ancient times (see Wilson, 1969 for a historical review). Wilby (1994) pointed out that "hierarchy theory has been deemed successful in the systems field" and "it is necessary and appropriate to critique the development and application of hierarchy theory". She went on to identify several difficulties with hierarchy theory, including: (1) the lack of a single, coherent

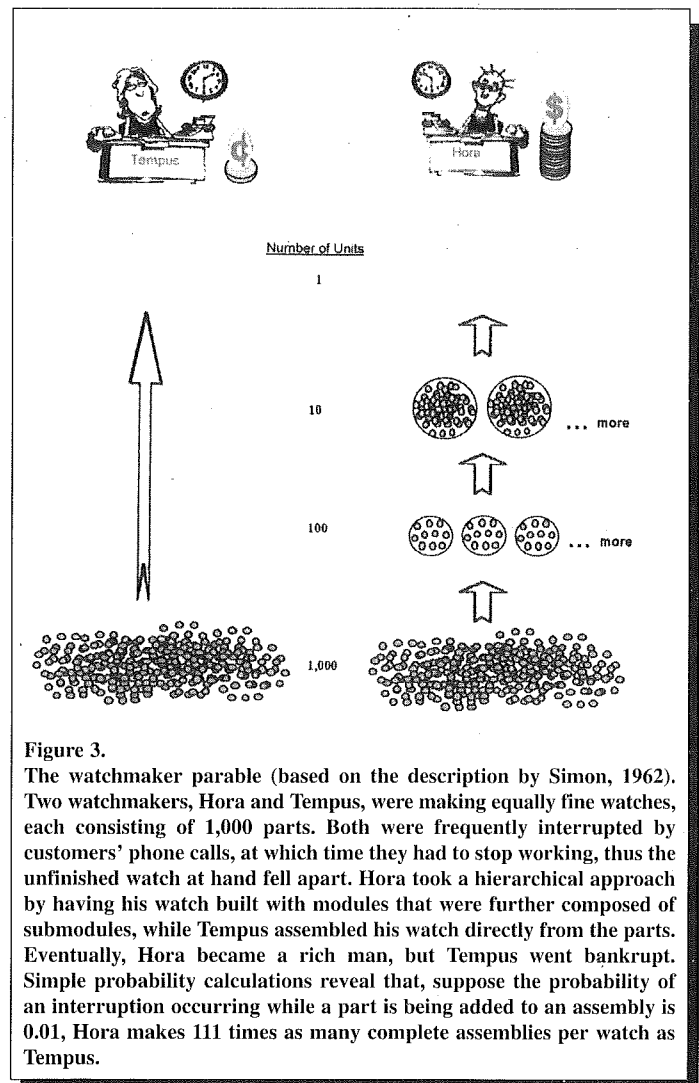


Figure 3.

The watchmaker parable (based on the description by Simon, 1962). Two watchmakers, Hora and Tempus, were making equally fine watches, each consisting of 1,000 parts. Both were frequently interrupted by customers' phone calls, at which time they had to stop working, thus the unfinished watch at hand fell apart. Hora took a hierarchical approach by having his watch built with modules that were further composed of submodules, while Tempus assembled his watch directly from the parts. Eventually, Hora became a rich man, but Tempus went bankrupt. Simple probability calculations reveal that, suppose the probability of an interruption occurring while a part is being added to an assembly is 0.01, Hora makes 111 times as many complete assemblies per watch as Tempus.

set of definitions and principles for all variants of the theory; (2) the lack of a specific, systematic methodology for the application of the theory; and (3) the lack of a precise and capable mathematical framework for the theory (also see O'Neill, 1989). While these criticisms are all relevant, as many have argued (e.g., Overton, 1975b; Turner *et al.*, 1989; Caldwell *et al.*, 1993; Reynolds *et al.*, 1993; Giampietro, 1994; Wu and Loucks, 1995; O'Neill, 1996; Reynolds and Wu, 1999), hierarchy theory can be used to facilitate understanding of the ecological complexity and developing scaling rules. In the following section, I shall discuss how hierarchy theory can be integrated with the theory of spatial heterogeneity, patch dynamics, to achieve such a goal.

HIERARCHICAL PATCH DYNAMICS (HPD)

Ecological systems are hierarchical patch mosaics. On different scales, a patch may be defined as a continent surrounded by oceans, a forest stand surrounded by agricultural lands and urban areas, a fire-burned area or a tree gap within a forest, or a stomata on a leaf. Patches can be characterized by their size,

shape, content, duration, structural complexity, and boundary characteristics. The theory of patch dynamics indicates that the structure, function, and dynamics of such patches are important to understanding the systems they comprise, be they populations, communities, ecosystems, or landscapes (see Levin and Paine, 1974; Pickett and White, 1985; Wu and Loucks, 1995; Pickett *et al.*, 1998). Since the 1970s, patch dynamics has become one of the most central perspectives in ecology. The hierarchical patch dynamics paradigm (HPDP; Wu and Loucks, 1995) integrates the theory of patch dynamics with hierarchy theory by expressing the relationship among pattern, process, and scale explicitly in the context of a landscape. The main points of HPDP include:

(1) Ecological systems can be perceived and studied as spatially-nested patch hierarchies, in which larger patches are made of smaller, functioning patches. The levels in these hierarchical patch systems are characterized by distinct characteristic scales or domains of scale, where patches at each level may correspond to holons (mosaics of smaller patches). The spatial structure of patch hierarchies are, in general, nearly decomposable. This suggests that patch boundaries at any scale may variably overlap with each other (Gosz, 1993; Fortin, 1994; Fortin and Drapeau, 1995). The significance of establishing such a patch hierarchy lies in the premise that spatial and temporal scales are fundamentally linked to each other, and that complex systems can be decomposed in time and space simultaneously (Simon and Ando, 1961; Courtois, 1985; Salthe, 1991; Giampietro, 1994). This is supported empirically by the fact that many physical and ecological phenomena arrange themselves, by and large, along the 45° line in a space-time scale diagram (Figure 4; also see Stommel, 1963; Delcourt and Delcourt, 1983, 1988; Clark, 1985; Urban *et al.*, 1987; Walker and Walker, 1991; Innes, 1998).

The hierarchical patch structure is a manifestation of the spatial pattern of ecological systems at different scales, and because it is tangible, it facilitates considerations of how pattern interacts with process across these scales. For example, Kolasa (1989; also see Kolasa and Waltho, 1998) developed a general conceptual model in which the structure of an environment, viewed as a nested hierarchy of habitat units, significantly determines the structure of biotic communities across scales. Based on statistical analysis of empirical data from eight different communities (e.g., flatworms, aquatic insects, foraminiferans, rodents, and birds), Kolasa (1989) was able to show the clusters, or "scale breaks", in community structure in terms of species abundance which corresponded nicely to the hierarchical habitat structure. Similarly, Kotliar and Wiens (1990) proposed a hierarchical patch model of habitat that emphasizes the perception and responses of organisms to spatial patchiness. Indeed, such a spatial patch hierarchy-based approach is successful in a variety of fields, including geography and soil science (e.g., Haigh, 1987; de Boer and Campbell, 1989), geomorphology (e.g., Phillips, 1995), remote sensing (e.g., Woodcock and Harward, 1992), and ecology (e.g., Urban *et al.*, 1987; Smith and Urban, 1988; Wu and Levin, 1994, 1997).

Because different organisms and ecological processes respond to patchiness at different scales, different patch hierarchies for them may be perceived even within the same landscape. In other words, there is no single correct patch hierarchy for all phenomena. Conceivably, only when most processes of interest respond to the structure at corresponding discrete levels is a patch hierarchy robust and effective for relating pattern to process and for scaling. In nature, the boundary-surfaces of different properties often tend to coincide with each other because many surfaces are mutually-reinforcing (Platt, 1969).

(2) Dynamics of a given ecological system can be derived from the dynamics of interacting patches at adjacent hierarchical levels. Patches at higher levels impose top-down constraints to those at lower levels by having slower, or less frequent, processes, while lower levels provide initiating conditions and mechanistic explanations for, and give apparent identity and integrity to, higher levels through interactions among components or holons (here patches). Distinctive characteristic time scales of patches at lower vs. higher levels are the fundamental reason for the near-decomposability of ecological systems. The structural decomposition can provide useful clues for the decomposition of processes or dynamics here, and the result of the latter should be used to refine and validate the former. Hierarchy theory indicates that, in general, the strength and frequency of interactions between levels decrease with distance. This means that, for a given phenomenon, a complex system with a large number of patches over a wide range of scales can be, and should be, reduced to a much simplified system with only a small number of discrete levels that are

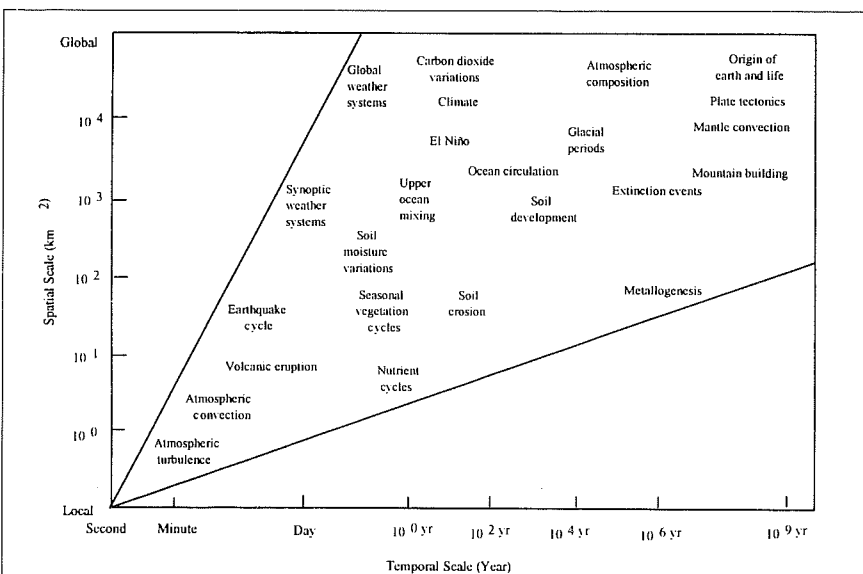


Figure 4. Physical and ecological phenomena tend to line up, approximately, along the diagonal direction in the space-time scale diagram although variations may sometimes be large (Redrawn from NASA, 1988; cited in Innes, 1998).

adjacent to each other. For hierarchical systems, an appropriate decomposition should only allow some, but an insignificant, amount of information loss. How much exactly? Aggregating a large number of components, or decomposing a complex system, into a smaller number of levels to study system dynamics is, in a way, similar to approximating the solutions of differential equations using a truncated Taylor series. The magnitude of the "truncation" errors depends not only on the method itself, but also on the nature of the processes (e.g., nonlinear interactions, feedbacks, time delays), spatial heterogeneity, and the scale of measurement or observation.

From hierarchy theory, three consecutive levels in the patch hierarchy should be considered to describe an ecological phenomenon for both comprehensiveness and conciseness: the focal patch level, and the ones immediately above and below it. Thus, if we write equations to describe the dynamics of the focal level, which corresponds to the characteristic scale of the phenomenon of interest, the level below it provides initiating conditions (or parameters as statistical averages), whereas the level above sets the boundary conditions (constants). Such a system description is not only most parsimonious, but also avoids the problems resulting from having too much detail in models: error aggregation, instability, enormous computational demands, and diminishing comprehensibility. These problems can be ameliorated to some extent by employing, for example, the object-oriented technology (Booch, 1994) when several levels are necessary to be considered simultaneously, but may never be completely eliminated.

(3) Pattern and process have components that are reciprocally related, and both pattern and process, as well as their relationship, change with scale. Different patterns and processes usually differ in the characteristic scales at which they operate. Again, this relates to the near-decomposability of ecological systems, and explains why they can be, and have been, studied at a variety of scales. To link patterns with processes at the same scale, or to translate them across scales, domains of scale (usually corresponding to hierarchical levels) need to be identified correctly. Establishing appropriate patch hierarchies facilitates understanding pattern and process and their relationships across scales.

(4) Nonequilibrium and stochastic processes are common in ecological systems. In general, small-scale processes tend to be more stochastic and less predictable. However, nonequilibrium and stochastic processes do not necessarily work against stability. They usually constitute mechanisms that underlie the apparent stability of ecological systems at a different scale (e.g., Urban *et al.*, 1987; Turner *et al.*, 1993; Wu and Levin, 1994). Thus, equilibrium and non-equilibrium are not absolute and context-free, but relative and scale-dependent. Furthermore, while high predictability and regularities can often be obtained within a single domain of scale in which similar processes dominate, one may speculate that unpredictability and irregularities will rise in the transitional zones between domains of scale (Wiens, 1989).

(5) Homeostatic stability is rarely observed in nature except for individual organisms, and persistent ecological systems usually exhibit metastability (homeorhetic, quasi-equilibrium

states). An important mechanism for achieving this metastability in hierarchical systems is incorporation, whereby nonequilibrium patch processes at one level translate to patterns and processes in a quasi-equilibrium state at a higher level (O'Neill *et al.*, 1986; Turner *et al.*, 1993; Wu and Levin, 1994). The concepts of incorporation and metastability emphasize multiple-scale processes and the consequences of heterogeneity.

A HIERARCHICAL PATCH DYNAMICS SCALING STRATEGY

Hierarchy theory suggests that complex systems have a high degree of redundancy, and description and understanding of them can be facilitated by simplifying them through decomposition into a limited number of subsystems. Plant life forms and functional groups (Smith *et al.*, 1997) are examples of aggregation (or decomposition) that makes use of redundancy in ecological systems to achieve simple descriptions and better understanding. Developing a hierarchy of landscape structural and functional units provides another example (Reynolds and Wu, 1999). Different simplifying schemes like those mentioned above can be used jointly with the HPD scaling strategy described below. For example, one highly sensible and powerful modelling and scaling scheme is the hierarchical ecosystem functional type (HEFT) approach that explicitly integrates hierarchical patch dynamics with the concept of ecosystem functional types (EFTs; see Reynolds *et al.*, 1997; Reynolds and Wu, 1999). Because the EFT concept emphasizes ecosystem attributes and processes (e.g., primary productivity, biogeochemical cycling, gas fluxes, hydrology), it provides concrete meanings to patches and thus reinforces the less tangible, but equally important, process aspect of the hierarchical patch dynamics paradigm.

In general, the hierarchical patch dynamics scaling strategy can be implemented in three stages, each of which may involve a number of steps and methods:

(1) Identifying Appropriate Patch Hierarchies

To identify patch hierarchies is to decompose complex spatial systems. In general, decomposing a complex system may invoke a top-down (partitioning) or bottom-up (aggregation) scheme or both. A top-down approach identifies levels and holons by progressively partitioning the entire system down-scale, whereas a bottom-up scheme involves successively aggregating or grouping similar entities upscale. Note that the difference between observational (scalar) and definitional (often non-scalar) hierarchies is not trivial (Ahl and Allen, 1996), because much of the power of hierarchy theory resides with the former. Therefore, although prescribed patch hierarchies, when corroborated empirically (e.g., Overton, 1975b; Reynolds *et al.*, 1993; Jarvis, 1995), can still be useful, quantitative methods, such as hierarchical partitioning (Chevan and Sutherland, 1991; MacNally, 1996), scale variance (Mollering and Tobler, 1972), multivariate statistical analyses, and spatial statistics, should be preferred for identifying patch hierarchies. For example, variability usually increases abruptly as transitions are approached between two neighbouring domains of scale

across a heterogeneous landscape, thus exhibiting “breaking points” or “spikes” in a scale analysis. These scale breaks, when verified, may characterize hierarchical levels. Since the upsurge of landscape ecology in North America in the 1980s, numerous methods of pattern analysis and spatial statistics have been developed to detect ecological scales (Turner *et al.*, 1991; Rossi *et al.*, 1992; Fortin and Drapeau, 1995; Gardner, 1998; Gustafson, 1998). For geographically large systems, remote sensing and geographic information systems are indispensable.

Besides pattern analysis and statistical methods mentioned above, cross-scale measurements or process modelling approaches can also be used to delineate patch boundaries. One example is illustrated by the following simple equation:

$$\frac{dS}{dt} = -D_h F_h + P - kS,$$

where dS/dt is the rate of change in a state variable S (e.g., nutrients, soil moisture, or biota) with respect to time, F_h is the horizontal flux of S ; $D_h F_h$ is the divergence of the horizontal flux F_h , and P and kS are the source and sink terms, respectively (Menzel *et al.*, 1999). When the study area increases successively, the horizontal flux divergence term may become rather large as compared to the other terms in the equation, indicating that lateral flows become significant. In this case, schemes of averaging over the land area may well result in considerable errors. Abrupt changes in the divergence term or dS/dt can thus be used to delineate patch boundaries. Raupach *et al.*, (1999) developed a similar formulation for tackling the problem of spatial complexity in modelling the interactions between vegetation and the atmosphere. They suggested that when the horizontal flux divergence term is significantly large, land-air exchange models can no longer consider just vertical fluxes or assume that the landscape under study is spatially homogeneous. In other words, at this time multiple patches must be explicitly considered due to nonlinear inter-patch interactions and feedbacks (i.e., spatial heterogeneity matters!). An excellent elucidation of when and how spatial patchiness affects ecophysiological and meteorological processes can be found in Baldocchi (1993) and Jarvis (1995).

As mentioned earlier, different phenomena, objectives, or criteria may result in different patch hierarchies, in terms of both the number of hierarchical levels, and their characteristic spatiotemporal scales. The criteria for identifying patch hierarchies should consider both structural and process characteristics pertinent to the phenomenon under study, although establishing a structural patch hierarchy is a logical first step. These tangible structural hierarchies should be modified and refined based on further analysis of relevant processes, because they only

become meaningful and powerful “scaling ladders” when the spatial and temporal scales of patches of each hierarchical level largely correspond to each other.

(2) Making Observations and Developing Models of Patterns and Processes Around Focal Levels

Once an appropriate patch hierarchy is established, patterns and processes can be studied at their characteristic scales or domains of scale, i.e., focal levels, by properly choosing grain and extent. The choice of grain and extent is critically important because they determine what can be observed (Allen *et al.*, 1984). There are always many factors existing in ecological systems, no matter what phenomena are to be studied, but not all of them deserve consideration. For example, soil evaporation and heat storage in soil and vegetation significantly affect the energy balance of a canopy, but not that of a leaf (Baldocchi, 1993). Simon (1973) gave a simple, but enlightening, example: if the total time span (extent) is set to T , and time interval (grain) to τ , for observing behaviour of a given level, high frequency (much greater than $1/\tau$) dynamics can be seen only as statistical averages, while low frequency (much less than $1/T$) dynamics will not be observed and thus will be treated as constants. Accordingly, mathematical models, involving only three adjacent levels and with relatively modest complexity, can be developed for addressing questions relevant to each domain of scale. These points seem to be equally valid when spatial grain and extent are considered. Information from scale analysis in identifying patch hierarchies can help choose appropriate grain and extent for each domain.

(3) Extrapolation Across the Domains of Scale Hierarchically

Now it is time to extrapolate information across domains of scale (or levels) along a patch hierarchy. This can be accomplished by changing grain, extent, or both (Figure 5). Specifically, scaling-up entails increasing extent or grain, or more commonly

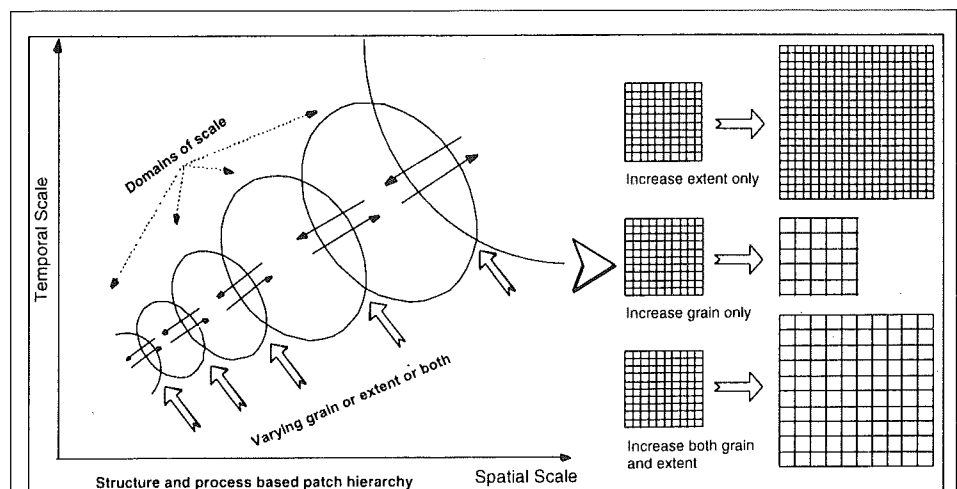


Figure 5. Hierarchical scaling or extrapolating information along a hierarchical scaling ladder. Scaling up or down is implemented by changing model grain size, extent, or both across successive domains of scale (see text for more details).

both, whereas scaling-down involves decreasing extent, grain, or more commonly both (Allen *et al.*, 1984; King, 1991). In either case, scaling requires multiple observation sets (*sensu* Allen *et al.*, 1984) made at different domains of scale. Based on the principles of loose vertical and horizontal coupling and near-decomposability, hierarchy theory suggests scaling with both grain and extent changed simultaneously and accordingly. This is very similar to the way human eyes work when moving away from an object (scaling up) or approaching it (scaling down). An interesting and profound message here is that to gain new information at a higher level, one needs to "hide" or suppress information at the lower levels. Again, one sees the importance of establishing patch hierarchies pertinent to the variables to be scaled. A properly identified spatial patch hierarchy serves as a "ladder" for scaling up or down (Figures 5 and 6). Such patch hierarchies should ideally emerge from analyses of observational data on both pattern and process. As pointed out earlier, prescribed hierarchies based on general empirical experience (e.g., individual-population-community; tree-stand-landscape-region) may also work for particular processes. However, we must bear in mind that prescribed hierarchies, though convenient, may prove to be inadequate or inappropriate for many processes or purposes.

Numerous methods exist for extrapolating information across adjacent scales in different fields of earth sciences (e.g., Iwasa *et al.*, 1987, 1989; Ehleringer and Field, 1993; Stewart *et al.*, 1996; van Gardingen *et al.*, 1997; Kunin, 1998). Particularly relevant here are those discussed by King (1991) and Jarvis (1995). Jarvis (1995) identified three approaches to scaling up experimental measurements: direct summation, averaging, and aggregation. The direct summation is simply the addition of measurements of ecological variables for all component patches in the study area. In most ecological systems, the structural and functional properties of patches vary among themselves and with scale. If we were able to measure these attributes for all patches simultaneously, simply adding them up would provide an accurate estimate for the entire landscape. However, this is apparently impractical for large, complex landscapes. The averaging scheme is to derive estimates at larger scales, based on appropriately calculated averages of relevant parameters that have been measured or estimated at a smaller scale. While both the summation and averaging methods treat the driving variables as independent variables, the aggregation approach takes into account the interactions between patches, feedbacks among components, and hierarchical linkages across scales, which can be facilitated by the HPD scaling strategy.

King (1991) identified four general methods for scaling up ecological models: (1) lumping, (2) direct extrapolation, (3) extrapolation by expected value, and (4) explicit integration. The first method, lumping, is the simplest method for scaling up ecological models by which coarse-scale mean values are derived from averaging fine-scale variables or parameters as both the model grain and extent usually are increased in the same time. Lumping assumes that the mathematical formulation of processes in smaller-scale models remains valid at larger

scales, or that larger-scale systems behave in the same, or a similar, way as the average fine-scale system. Scaling up can also be accomplished by increasing the model extent only while holding the model grain constant (see Allen *et al.*, 1984), and the second and third method discussed by King (1991) follow such an scheme. Direct extrapolation, the second method, is to apply the same local small-scale model to each patch in the landscape for which the model is appropriate and then to compute the (area-weighted) summation of the output from all the patches as the estimate for the entire landscape. This is essentially the approach used in many spatially-explicit regional ecosystem or landscape models. Direct extrapolation is subject to spatial aggregation errors and may suffer when the small-scale model is computationally intensive or the number of patches in the landscape is huge.

The third method is extrapolation by expected value in which large-scale estimates are obtained from multiplying the landscape area by the expected value of the output from the small-scale models applied across a spatially heterogeneous area. In this case, model arguments (state variables, parameters, and driving variables) that vary spatially are treated as random variables. That is:

$$Y = AE[f(x,p,z)] = AE[y]$$

where Y is the landscape expression of local behaviour, y; A is the landscape area; E[] is the expected value operator; f is the local model; and x, p, and z are vectors of state variables, parameters, and driving variables, respectively. Both direct extrapolation and extrapolation by expected value methods scale up by increasing the model extent, without altering the structure of the small-scale model. King (1991) indicated a couple of key issues in employing these two methods: (1) appropriately describing landscape heterogeneity with respect to the arguments of the local scale model, and (2) appropriately combining output from the local scale model to derive the aggregate expression for the landscape. The fourth method, extrapolation by explicit integration, is accomplished by explicitly evaluating the integral of the smaller-scale model with respect to space in closed form. This requires that the small-scale model be defined as a mathematical function of space and also be integrable. In contrast with the second and third methods, the structure of the local-scale model changes as a function of space in the method of extrapolation by explicit integration, and the problem of model grain disappears because the landscape is essentially treated as a continuous surface. This approach apparently is mathematically more tractable and computationally efficient, but difficulties in representing spatially heterogeneous landscapes as continuous functions in exact forms may seriously limit its applicability.

From the above discussion, it becomes clear that a diversity of existing specific scaling methods can be used in the third stage of the hierarchical patch dynamics scaling strategy. While the HPD scaling strategy is based on, and complements, these earlier studies, it differs from them in its generality and the emphasis on hierarchical structure of nature.

Is it possible to extrapolate information across a wide range of scales, and if so, how? Hierarchy theory may suggest that such an endeavour is not necessary for understanding and predicting many ecological phenomena. Conceptually, this is because the flows of matter, energy, and information across hierarchical levels are successively filtered by surfaces, so that the details at one level will eventually become irrelevant or undetectable at a distant level. However, if there is a need for scaling up from the leaf to the globe, it is preferable to develop a hierarchy of hierarchical models that each contain three adjacent levels, which together allow for translating information across a wide range of scales. These "unit" hierarchical models then can be chained in an input-out fashion to reach the total length of the patch hierarchy (e.g., Reynolds *et al.*, 1993, Jarvis, 1995; Reynolds and Wu, 1999). **Figure 6** is a schematic illustration of such an approach, depicting the processes of decomposing complexity, establishing a patch hierarchy based on pattern and process, building a hierarchy of unit hierarchical models, and scaling up models through an input-output chain while incorporating both bottom-up mechanisms and top-down constraints. The object-oriented technology (object-oriented analysis, object-oriented design, and object-oriented programming; see Booch, 1994) seems to have much to offer to facilitate the development of such hierarchical models.

DISCUSSION AND CONCLUSIONS

Scaling is ubiquitous in ecological studies, although we may not always realize it explicitly. In fact, whenever averages of ecological variables are used, a certain kind of aggregation or

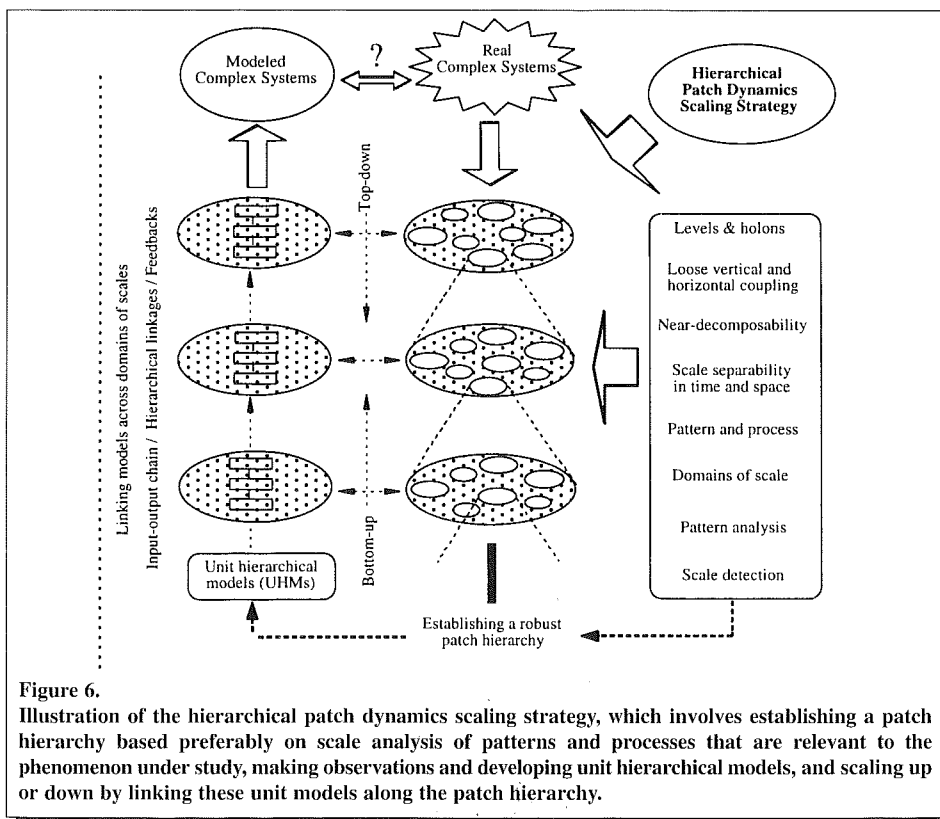
scaling over space or time is performed. While scaling has acutely been recognized as one of the most important and pressing challenges across all fields of earth sciences (see Wiens, 1989; Ehleringer and Field, 1993; King, 1991; Levin, 1992; Rastetter *et al.*, 1992; Jarvis, 1995; Wu and Loucks, 1995; Stewart *et al.*, 1996; van Gardingen *et al.*, 1997; Peterson and Parker, 1998), scaling rules or systematic scaling methods are scarce, especially when heterogeneous landscapes are considered.

Ecologists are acutely aware that spatial heterogeneity matters, and that nonlinearity rules. Recognizing, identifying, and taking advantage of the hierarchical structure and near-decomposability of complex ecological systems may hold the key to understanding and prediction through robust simplification and successful scaling. Hierarchy theory suggests that it would be difficult, if ever possible, to translate information directly between two distant domains when there exist intervening levels that are relevant to the chosen phenomenon, but which are ignored (Allen *et al.*, 1984). O'Neill *et al.*, (1986) reiterated this important point: "Any attempt to relate a macroscopic property to the detailed behaviours of components several layers lower in the hierarchy is bound to fail due to the successive filtering".

The hierarchical patch dynamics paradigm, integrating hierarchy theory and patch dynamics, allows us to simplify the complexity of nature, yet to retain its essence. Scaling up and down both can be open-ended, which in a way reminds us of what to expect from an unclosed system of equations with a number of free parameters. The hierarchical patch dynamics scaling scheme provides a conceptual basis for closing up the open ends when we move up or down scales in space and time.

In particular, the HPD scaling strategy provides a ladder for scaling. I argue that, if it is possible to scale up from the cell to the globe, most likely this has to be done through a hierarchical approach. Using a "scaling ladder" should greatly enhance the feasibility and minimize the danger of errors in translating information across a wide range of scales.

Currently, we are using the HPD scheme to develop models and scale up pattern and process in arid landscapes, including the Phoenix metropolitan area (through the Central Arizona – Phoenix Long-Term Ecological Research project). While the benefits of using the HPD approach in terms of conceptualizing complex problems and organizing massive data for these systems are evident, more in-depth and comprehensive examinations of its strengths and weaknesses in terms of facilitating understanding and scaling still need to be, and will be, done through these and other related studies.



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REFERENCES

- Ahl, V., and T.F.H. Allen. 1996. *Hierarchy Theory: A Vision, Vocabulary, and Epistemology*. Columbia University Press, New York.
- Allen, T.F.H., and T.W. Hoekstra. 1992. *Toward a Unified Ecology*. Columbia University Press, New York.
- Allen, R.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 Tech Report RM-110. Rocky Mountain Forest and Range Experiment Station.
- Allen, T.F.H., and T.B. Starik. 1982. *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago.
- Ando, A., and F.M. Fisher. 1963. "Near-Decomposability, Partition and Aggregation, and the Relevance of Stability Discussions". *International Economic Review*, 4:53-67.
- Baldocchi, D.D. 1993. "Scaling Water Vapor and Carbon Dioxide Exchange from Leaves to a Canopy: Rules and Tools". In J.R. Ehleringer and C.B. Field (eds.), *Scaling Physiological Processes: Leaf to Globe*, pp. 77-114. Academic Press, San Diego.
- Bartell, S.M., W.G. Cale, R.V. O'Neill, and R. H. Gardner. 1988. "Aggregation Error: Research Objectives and Relevant Model Structure". *Ecological Modelling*, 41:157-168.
- Booch, G. 1994. *Object-Oriented Analysis and Design with Applications*. Second ed. Addison-Wesley, Reading.
- Caldwell, M.M., P.A. Matson, C. Wessman, and J. Gamon. 1993. "Prospects for Scaling". In J.R. Ehleringer and C.B. Field (eds.), *Scaling Physiological Processes: Leaf to Globe*, pp. 223-229. Academic Press, San Diego.
- Cale, W.G., and P.L. Odell. 1979. "Concerning Aggregation in Ecosystem Modeling". In E. Halfon (ed.), *Theoretical Systems Ecology*, pp. 55-77. Academic Press, New York.
- Cale, W.G., R.V. O'Neill, and R. H. Gardner. 1983. "Aggregation Error in Nonlinear Ecological Models". *Journal of Theoretical Biology*, 100:539-550.
- Carpenter, S.R., S.W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. "Ecosystem Experiments". *Science*, 269:324-327.
- Chevan, A., and M. Sutherland. 1991. "Hierarchical Partitioning". *American Statistician*, 45:90-96.
- Clark, W.C. 1985. "Scales of Climate Impacts". *Climatic Change*, 7:5-27.
- Courtois, P.J. 1985. "On Time and Space Decomposition of Complex Structures". *Communications of the ACM*, 28:590-603.
- de Boer, D.H., and I.A. Campbell. 1989. "Spatial Scale Dependence of Sediment Dynamics in a Semi-Arid Badland Drainage Basin". *Catena*, 16:277-290.
- Delcourt, H.R., and P.A. Delcourt. 1988. "Quaternary Landscape Ecology: Relevant Scales in Space and Time". *Landscape Ecology*, 2:23-44.
- Delcourt, H.R., P.A. Delcourt, and T. Webb. 1983. "Dynamic Plant Ecology: The Spectrum of Vegetational Change in Space and Time". *Quaternary Science Reviews*, 1:153-175.
- Ehleringer, J.R., and C.B. Field. 1993. *Scaling Physiological Processes: Leaf to Globe*, pp. 388. Academic Press, San Diego.
- Fisher, F.M. 1963. "Decomposability, Near Decomposability, and Balanced Price Change Under Constant Returns to Scale". *Econometrica*, 31:67-89.
- Flood, R.L. 1987. "Complexity: A Definition by Construction of a Conceptual Framework". *Systems Research*, 4:177-185.
- Flood, R.L., and E.R. Carson. 1993. *Dealing with Complexity: An Introduction to the Theory and Application of Systems Science*. 2nd ed. Plenum Press, New York.
- Fortin, M.-J. 1994. "Edge Detection Algorithms for Two-Dimensional Ecological Data". *Ecology*, 75:956-965.
- Fortin, M.-J., and P. Drapeau. 1995. "Delineation of Ecological Boundaries: Comparison of Approaches and Significance Tests". *Oikos*, 72:323-332.
- Gardner, R.H. 1998. "Pattern, Process, and the Analysis of Spatial Scales". In D.L. Peterson and V.T. Parker (eds.), *Ecological Scale: Theory and Applications*, pp. 17-34. Columbia University Press, New York.
- Gardner, R.H., W.G. Cale, and R. V. O'Neill. 1982. "Robust Analysis of Aggregation Error". *Ecology*, 63:1771-1779.
- Giampietro, M. 1994. "Using Hierarchy Theory to Explore the Concept of Sustainable Development". *Futures*, 26:616-625.
- Gosz, J.R. 1993. "Ecotone Hierarchies". *Ecological Applications*, 3(3):369-376.
- Gustafson, E.J. 1998. "Quantifying Landscape Spatial Pattern: What is the State of the Art?" *Ecosystems*, 1:143-156.
- Haigh, M.J. 1987. The Holon: Hierarchy Theory and Landscape Research". *Catena Supplement*, 10:181-192.
- Heuvelink, G.B.M., P.A. Burrough, and A. Stein. 1989. "Propagation of Errors in Spatial Modelling with GIS". *International Journal of Geographical Information Systems*, 3:303-322.
- Hiebeler, D. 1997. "Stochastic Spatial Models: From Simulations to Mean Field and Local Structure Approximations". *Journal of Theoretical Biology*, 187:307.
- Holling, C.S. 1992. "Cross-Scale Morphology, Geometry, and Dynamics of Ecosystems". *Ecological Monographs*, 62:447-502.
- Innes, J.L. 1998. "Measuring Environmental Change". In D. L. Peterson and V. T. Parker (eds.), *Ecological Scale: Theory and Applications*, pp. 429-457. Columbia University Press, New York.
- Iwasa, Y., V. Andreasen, and S.A. Levin. 1987. "Aggregation in Model Ecosystems: I. Perfect Aggregation". *Ecological Modelling*, 37:287-302.

- Iwasa, Y., S.A. Levin, and V. Andreasen. 1989. "Aggregation in Model Ecosystems: II. Approximate Aggregation. IMA" *Journal of Mathematics Applied in Medicine & Biology*, 6:1-23.
- Jarvis, P.G. 1995. "Scaling Processes and Problems". *Plant, Cell and Environment*, 18:1079-1089.
- Kareiva, P., and M. Andersen. 1986. "Spatial Aspects of Species Interactions: The Wedding of Models and Experiments". In A. Hastings (ed.), *Community Ecology*, pp. 35-50. Springer-Verlag, Berlin.
- King, A. 1991. "Translating Models Across Scales in the Landscape". In M.G. Turner and R.H. Gardner (eds.), *Quantitative Methods in Landscape Ecology*, pp. 479-517. Springer-Verlag, New York.
- King, A.W., A.R. Johnson, and R.V. O'Neill. 1991. "Transmutation and Functional Representation of Heterogeneous Landscapes". *Landscape Ecology*, 5:239-253.
- Klir, G. 1985. "Complexity: Some General Observations". *Systems Research*, 2:131-140.
- Koestler, A. 1967. *The Ghost in the Machine*. Random House, New York.
- Kolasa, J. 1989. "Ecological Systems in Hierarchical Perspective: Breaks in Community Structure and Other Consequences". *Ecology*, 70:36-47.
- Kolasa, J., and N. Waltho. 1998. "A Hierarchical View of Habitat and Its Relationship to Species Abundance". In D.L. Peterson and V.T. Parker (eds.), *Ecological Scale: Theory and Applications*, pp. 55-76. Columbia University Press, New York.
- Kotliar, N.B., and J.A. Wiens. 1990. "Multiple Scales of Patchiness and Patch Structure: A Hierarchical Framework for the Study of Heterogeneity." *Oikos*, 59:253-260.
- Kunin, W.E. 1998. "Extrapolating Species Abundance Across Spatial Scales". *Science*, 281:1513-1515.
- Levin, S.A. 1992. "The Problem of Pattern and Scale in Ecology". *Ecology*, 73:1943-1967.
- Levin, S.A., and R.T. Paine. 1974. "Disturbance, Patch Formation and Community Structure". *Proceedings of the National Academy of Sciences*, 71:2744-2747.
- MacNally, R. 1996. "Hierarchical Partitioning as an Interpretative Tool in Multivariate Inference". *Australian Journal of Ecology*, 21:224-228.
- Menzel, L., O. Richter, N.E. Caraco, G.M. Hornberger, R.B. Jackson, C.A. Johnston, H. Lang, and E.F. Wood. 1999. "How is Ecosystem Function Affected by Hydrological Lateral Flows in Complex Landscapes?" In J.D. Tenhunen and P. Kabat (eds.), *Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes*. John, Wiley, In press.
- Mesarovic, M.D., D. Macko, and Y. Takahara. 1970. *Theory of Hierarchical, Multilevel, Systems*. Academic Press, New York.
- Miller, G. 1956. "The Magical Number Seven, Plus or Minus Two: Some Limits on Our Capacity for Processing Information". *The Psychological Review*, 63:86-100.
- Miller, J.G. 1978. *Living Systems*. McGraw-Hill, New York.
- Moellering, H., and W. Tobler. 1972. "Geographical Variances". *Geographical Analysis*, 4:34-64.
- Morrison, P. 1966. "The Modularity of Knowing". In G. Kepes (ed.), *Module, Proportion, Symmetry, Rhythm*, pp. 1-19. Braziller, New York.
- NASA Advisory Council, Earth System Science Committee. 1988. *Earth System Science: A Closer View*. National Aeronautics and Space Administration, Washington, D.C.
- Newell, A., and H. A. Simon. 1972. *Human Problem Solving*. Prentice-Hall, Englewood Cliffs.
- O'Neill, R.V. 1988. "Hierarchy Theory and Global Change". In T. Rosswall, R. G. Woodmansee and P. G. Risser (eds.), *Scales and Global Change*, pp. 29-45. John Wiley & Sons, New York.
- O'Neill, R.V. 1989. "Perspectives in Hierarchy and Scale". In J. Roughgarden, R. M. May and S. A. Levin (eds.), *Perspectives in Ecological Theory*, pp. 140-156. Princeton University Press, Princeton.
- O'Neill, R.V. 1996. "Recent Developments in Ecological Theory: Hierarchy and Scale". In J. M. Scott, T. H. Tear and F. W. Davis (eds.), *GAP Analysis: A Landscape Approach to Biodiversity Planning*, pp. 7-14. American Society of Photogrammetry & Remote Sensing, Bethesda.
- 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.
- O'Neill, R.V., and A.W. King. 1998. "Homage to St. Michael; or, Why Are There So Many Books on Scale?" In D. L. Peterson and V. T. Parker (eds.), *Ecological Scale: Theory and Applications*, pp. 3-15. Columbia University Press, New York.
- O'Neill, E.G., R.V. O'Neill, and R.J. Norby. 1991. "Hierarchy Theory as a Guide to Mycorrhizal Research on Large-Scale Problems". *Environmental Pollution*, 73:271-284.
- O'Neill, R.V., and B. Rust. 1979. Aggregation error in ecological models. *Ecological Modelling*, 7:91-105.
- Overton, W.S. 1975a. "Decomposability: A Unifying Concept?" In S. A. Levin (ed.), *Ecosystem Analysis and Prediction*, pp. 297-299. SIAM-SIMS, Philadelphia.
- Overton, W.S. 1975b. "The Ecosystem Modeling Approach in the Coniferous Forest Biome". In B. C. Patten (ed.), *Systems Analysis and Simulation in Ecology*, pp. 117-138. Academic Press, New York.
- Pattee, H.H. 1973. *Hierarchy Theory: The Challenge of Complex Systems*, pp. 156. George Braziller, New York.
- Paw U, K.T., R.H. Shaw, and T.P. Meyers. 1985. "Evapotranspiration as Modeled by a Higher Order Closure Scheme, Advances in Evapotranspiration". *Proceedings of the National Conference on Advances in Evapotranspiration*, pp. 43-50. American Society of Agricultural Engineers, Chicago.
- Peterson, D.L., and V.T. Parker. 1998. *Ecological Scale: Theory and Applications*, pp. 615. Columbia University Press, New York.
- Phillips, J.D. 1995. "Biogeomorphology and Landscape Evolution: The Problem of Scale". *Geomorphology*, 13:337-347.
- Pickett, S.T.A., and P.S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando.
- Pickett, S.T.A., J. Wu, and M.L. Cadenasso. 1999. "Patch Dynamics and the Ecology of Disturbed Ground". In L. R. Walker (ed.), *Ecosystems of the World: Ecosystems of Disturbed Ground*. Elsevier Science Publishers.
- Platt, J. 1969. "Theorems on Boundaries in Hierarchical Systems". In L.L. Whyte, A.G. Wilson and D. Wilson (eds.), *Hierarchical Structures*, pp. 201-213. American Elsevier, New York.
- Rastetter, E.B., A. W. King, B.J. Cosby, G.M. Hornberger, R.V. O'Neill, and J.E. Hobbi. 1992. "Aggregating Fine-Scale Ecological Knowledge to Model Coarser-Scale Attributes of Ecosystems". *Ecological Applications*, 2:55-70.

- Raupach, M.R., D.D. Baldocchi, H.-J. Bolle, L. Dümenil, W. Eugster, F.X. Meixner, J.A. Olejnik, R.A. Pielke, J.D. Tenhunen, and R. Valentin. 1999. "How is the Atmospheric Coupling of Land Surfaces Affected by Topography, Complexity in Landscape Patterning, and the Vegetation Mosaic?" In J.D. Tenhunen and P. Kabat (eds.), *Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes*. John Wiley.
- Reynolds, J.F., D.W. Hilbert, and P.R. Kemp. 1993. "Scaling Ecophysiology from the Plant to the Ecosystem: A Conceptual Framework". In J. R. Ehleringer and C. B. Field (eds.), *Scaling Physiological Processes: Leaf to Globe*, pp. 127-140. Academic Press, San Diego.
- Reynolds, J.F., R.A. Virginia, and W.H. Schlesinger. 1997. "Defining Functional Types for Models of Desertification". In T. M. Smith, H. H. Shugart and F.I. Woodward (eds.), *Plant Functional Types*, pp. 195-216. Cambridge University Press, Cambridge.
- Reynolds, J.R., and J. Wu. 1999. "Do Landscape Structural and Functional Units Exist?" In J.D. Tenhunen and P. Kabat (eds.), *Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes*, pp. 275-298. John Wiley, New York.
- Rossi, R.E., D.J. Mulla, A.G. Journel, and E.H. Franz. 1992. "Geostatistical Tools for Modeling and Interpreting Ecological Spatial Dependence". *Ecological Monographs*, 62:277-314.
- Salthe, S.N. 1985. *Evolving Hierarchical Systems: Their Structure and Representation*. Columbia University Press, New York.
- Salthe, S.N. 1991. "Two Forms of Hierarchy Theory in Western Discourses". *International Journal of General Systems*, 18:251-264.
- Schaffer, W.M. 1981. "Ecological Abstraction: The Consequences of Reduced Dimensionality in Ecological Models". *Ecological Monographs*, 51:383-401.
- Simon, H.A. 1962. "The Architecture of Complexity". *Proceedings of the American Philosophical Society*, 106:467-482.
- Simon, H.A. 1973. "The Organization of Complex Systems". In H.H. Pattee (ed.), *Hierarchy Theory: The Challenge of Complex Systems*, pp. 1-27. George Braziller, New York.
- Simon, H.A. 1996. *The Sciences of the Artificial*. 3rd ed. The MIT Press, Cambridge.
- Simon, H.A., and A. Ando. 1961. "Aggregation of Variables in Dynamic Systems". *Econometrica*, 29:111-138.
- Smith, T.M., H.H. Shugart, and F. I. Woodward. 1997. *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*, pp. 369. Cambridge University Press, Cambridge.
- Smith, T.M., and D.L. Urban. 1988. "Scale and Resolution of Forest Structural Pattern". *Vegetatio*, 74:143-150.
- Stewart, J.B., E.T. Engman, R.A. Feddes, and Y. Kerr. 1996. *Scaling up in Hydrology Using Remote Sensing*, pp. 255. John Wiley & Sons, Chichester.
- Stommel, H. 1963. "Varieties of Oceanographic Experience". *Science*, 139:572-576.
- Tilman, D. 1989. "Ecological Experimentation: Strengths and Conceptual Problems". In G. E. Likens (ed.), *Long-Term Studies in Ecology Approaches and Alternatives*, pp. 136-157. Springer-Verlag, New York.
- Turner, M.G., V.H. Dale, and R.H. Gardner. 1989. "Predicting Across Scales: Theory Development and Testing". *Landscape Ecology*, 3:245-252.
- Turner, M.G., W.H. Romme, R.H. Gardner, R.V. O'Neill, and T.K. Kratz. 1993. "A Revised Concept of Landscape Equilibrium: Disturbance and Stability on Scaled Landscapes". *Landscape Ecology*, 8:213-227.
- Turner, S.J., R.V. O'Neill, W. Conley, M.R. Conley, and H.C. Humphries. 1991. "Pattern and Scale: Statistics for Landscape Ecology". In M.G. Turner and R.H. Gardner (eds.), *Quantitative Methods in Landscape Ecology*, pp. 17-49. Springer-Verlag, New York.
- Urban, D.L., R.V. O'Neill, and J. Shugart, H.H. 1987. "Landscape Ecology". *BioScience*, 37:119-127.
- van Gardingen, P.R., G.M. Foody, and P.J. Curran. 1997. *Scaling-Up: From Cell to Landscape*, pp. 386. Cambridge University Press, Cambridge.
- Walker, D.A., and M.D. Walker. 1991. "History and Pattern of Disturbance in Alaskan Arctic Terrestrial Ecosystems: A Hierarchical Approach to Analysing Landscape Change". *Journal of Applied Ecology*, 28:244-276.
- Weaver, W. 1948. "Science and Complexity". *American Scientist*, 36:536-544.
- Weinberg, G.M. 1975. *An Introduction to General Systems Thinking*. John Wiley & Sons, New York.
- Weiss, P.A. 1971. *Hierarchically Organized Systems in Theory and Practice*. Hafner Publishing Company, New York.
- Whyte, L.L., A.G. Wilson, and D. Wilson. 1969. *Hierarchical Structures*, pp. 322. American Elsevier, New York.
- Wiens, J.A. 1989. "Spatial Scaling in Ecology". *Functional Ecology*, 3:385-397.
- Wilby, J. 1994. "A Critique of Hierarchy Theory". *Systems Practice*, 7:653-670.
- Wilson, D. 1969. "Forms of Hierarchy: A Selected Bibliography". In L.L. Whyte, A.G. Wilson and D. Wilson (eds.), *Hierarchical Structures*, pp. 287-314. American Elsevier, New York.
- Woodcock, C., and V.J. Harward. 1992. "Nested-Hierarchical Scene Models and Image Segmentation". *International Journal of Remote Sensing*, 13:3167-3187.
- Wu, J. 1990. "Modelling the Energy Exchange Processes Between Plant Communities and Environment". *Ecological Modelling*, 51:233-250.
- Wu, J., and S.A. Levin. 1994. "A Spatial Patch Dynamic Modeling Approach to Pattern and Process in an Annual Grassland". *Ecological Monographs*, 64(4):447-464.
- Wu, J., and O. L.Loucks. 1995. "From Balance-of-Nature to Hierarchical Patch Dynamics: A Paradigm Shift in Ecology". *Quarter Review of Biology*, 70:439-466.
- Wu, J. and S. A. Levin. 1997. "A Patch-Based Spatial Modeling Approach: Conceptual Framework and Simulation Scheme". *Ecological Modelling*, 101:325-346.