FROM BALANCE OF NATURE TO HIERARCHICAL PATCH DYNAMICS: A PARADIGM SHIFT IN ECOLOGY

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ABSTRACT

A common assumption historically in ecology is evident in the term "balance of nature." The phrase usually implies that undisturbed nature is ordered and harmonious, and that ecological systems return to a previous equilibrium after disturbances. The more recent concepts of point equilibrium and static stability, which characterize the classical equilibrium paradigm in ecology, are traceable to the assumptions implicit in "balance of nature." The classical equilibrium view, however, has failed not only because equilibrium conditions are rare in nature, but also because of our past inability to incorporate heterogeneity and scale multiplicity into our quantitative expressions for stability. The theories and models built around these equilibrium and stability principles have misrepresented the foundations of resource management, nature conservation, and environmental protection.

In this paper, we synthesize recent developments that advance our understandings of equilibrium vs. nonequilibrium, homogeneity vs. heterogeneity, determinism vs. stochasticity, and single-scale phenomenon vs. hierarchical linkages in ecological systems. The integration of patch dynamics with hierarchy theory has led to new perspectives in spatial and temporal dynamics, with explicit linkage between scale and heterogeneity. The major elements of the hierarchical patch dynamics paradigm include the idea of nested hierarchies of patch mosaics, ecosystem dynamics as a composite of patch changes in time and space, the pattern-process-scale perspective, the nonequilibrium perspective, and the concepts of incorporation and metastability. Both environmental stochasticities and biotic feedback interactions can cause instability and contribute to the dynamics observed at various scales. Stabilizing mechanisms that dampen these destabilizing forces include spatial incorporation, environmental disturbances, biological compensatory mechanisms, and heterogeneity absorption. Hierarchical patch dynamics incorporates certain "emergent properties" of ecological systems, such as metastability or persistence at the meta-scale, as opposed to the transient dynamics that usually characterize local phenomena. In contrast to the stability that derives from an assumed self-regulation in a closed system, the concepts of incorporation and metastability deal explicitly with multiple-scale processes and the consequences of heterogeneity. The most important contribution of hierarchical patch dynamics lies in the framework provided for explicitly incorporating heterogeneity and scale, and for integrating equilibrium, multiple equilibrium, and nonequilibrium perspectives.

"The balance of nature" does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude. Each variation in the numbers of one species causes direct and indirect repercussions on the numbers of the others, and since many of the latter are themselves independently varying in numbers, the resultant confusion is remarkable.

— *Charles Elton (1930)*

INTRODUCTION

THE IDEA of the balance of nature has been a long-standing element of Western tradition (DeAngelis and Waterhouse, 1987; O'Neill et al., 1986). In the Orient, slightly different ideas of unity, interplay, and harmony are central to the ancient Chinese philosophy of yin (Earth) and yang (Heaven), which has influenced Chinese medicine, agriculture, art, ethics, and natural sciences. This philosophy echoes the balance of nature concept by asserting that the universe is in harmony as a result of the balance between opposing but interdependent forces. Western society, on the other hand, has perceived the earth in various ways — as having a divine order, as a fellow creature, or as giant machinery (Egerton, 1973; Botkin, 1990). Such ideas have shaped our perception of nature. In particular, the balance of nature has been an implicit assumption in ecology for centuries, and thus has influenced both its theory and its practice (Egerton, 1973; Botkin, 1980, 1990; Pickett et al., 1992; Wu, 1992). We have come to use the ideas of stability and equilibrium to convey this assumption. Populations, communities, ecosystems, and even the entire earth have been viewed as potentially self-regulating systems that are kept in a stable equilibrium by predictable forces if left alone (e.g., Nicholson, 1933; Milne and Milne, 1960; Lovelock, 1987).

Many ecologists have challenged the idea of the balance of nature and the related concepts of equilibrium and stability since the early period of this century (e.g., Elton, 1930; Ehrlich and Birch, 1967; Botkin and Sobel, 1975; Caswell, 1978; Chesson and Case, 1986; Pickett et al., 1992; Wu, 1992). Botkin (1990) even asserted that understanding of the natural world and our ability to solve environmental problems may be limited significantly by such age-old myths and metaphors. But if stability and equilibrium concepts do not hold, is there any basis for the widely held beliefs in balance and harmony, and is there an alternative paradigm?

A better understanding of the relationship between equilibrium and nonequilibrium components in ecological systems requires consideration of the heterogeneity and multiplicity in spatial and temporal dimensions. Both natural and anthropogenic factors or processes generate patchiness in nature across a wide range of spatial and temporal scales. Our ability to understand and predict the dynamics of ecological systems may have been hindered not only by the historical roots of the balance of nature assumption, but also by other factors. Although ecological patterns and processes exhibit scale-varying heterogeneity, traditional ecological approaches fail to consider the outcomes of such scale dependencies and patchiness. In addition, traditional methodologies tend to be polarized either towards reductionism or holism, neither of which captures the multiply scaled, hierarchical processes of ecological systems. Functional approaches in ecology typically emphasize processes, paying limited attention to the effects of spatial pattern, while structural approaches are concerned largely with spatial or temporal change or pattern. A new conceptual framework is needed that could free ecological theory from the balance of nature assumption and the extremes of holism and reductionism. The hierarchical patch dynamics paradigm has been emerging from the integration of several recent developments in ecology, and fills this need.

We use the term "paradigm" to indicate a constellation of concepts, ideas, approaches, and principles shared and used by a scientific community to define research problems and solutions (Kuhn, 1970; Capra, 1986). At its emerging stage, a new paradigm may appear nebulous as to its structural elements and predictive capacity. As Capra (1986) pointed out, "During a paradigm shift, the new paradigm

first emerges in outline," and "will establish itself when a synthesis is produced that is sufficiently attractive to a large number of people in the community." Also, a paradigm is only a partial view of the world (O'Neill, 1995), so both merits and limitations should be expected. We argue that hierarchical patch dynamics represents a new approach to the ideas of equilibrium, stability and system regulation in particular, and structure, function and dynamics of ecological systems in general. The main objective of this paper is to explore the changing perspectives and approaches that have led to a paradigm shift, and to focus on the explanatory power of the new perspective. We first review the early significance of the idea of balance in nature, and discuss the classical equilibrium paradigm and its problems. We then consider several nonequilibrium and multiple equilibrium perspectives. Based on these reviews, we explore the main elements of the hierarchical patch dynamics paradigm and its implications.

BALANCE OF NATURE AND THE CLASSICAL ECOLOGICAL PARADIGM

The idea of the balance of nature emerged implicitly in western antiquity; it is evident in early Greek cosmologies, and has evolved in multiple forms since then (see Egerton, 1973 for a comprehensive review). It has been a background assumption in ecology for centuries (Egerton, 1973; McIntosh, 1985; Botkin, 1990; Pimm, 1991). Carl Linnaeus gave this idea its first name, "oeconomia naturae," in 1749 (Egerton, 1973). The central idea was transformed later from "a natural order," given by divine providence, to an order generated and maintained by nature through evolution (Egerton, 1973; McIntosh, 1980, 1985). The supraorganismic implication of the balance of nature also may have suggested to some that nature itself was a supraorganism, with all living things being its organs. Many pioneers in the 19th century, including Charles Darwin, George P. Marsh, and Stephen A. Forbes, all evidenced a belief that nature could be understood in terms of the balance of destructive and conservative forces, and that nature would maintain a permanence of structure and function if left undisturbed (Botkin, 1980; McIntosh, 1985). In

the 20th century, Clements (1916) argued strongly for the supraorganismic concept of the plant community. His viewpoint has been cited repeatedly as a direct outcome of the balance of nature tradition (e.g., Simberloff, 1980; Botkin, 1990).

In spite of criticisms of the balance of nature assumption in population and community regulation (e.g., Gleason, 1926; Elton, 1930), the idea remains prominent in modern ecology. The modern derivatives, such as equilibrium, steady-state, stability, and homeostasis, are central concepts of the classical equilibrium paradigm (McIntosh, 1980, 1985; DeAngelis and Waterhouse, 1987; Botkin, 1990), which dominated ecological thought during the 1960s and 1970s. The persistence of these concepts also can be attributed to theories and methods borrowed from 19th and 20th century physics and engineering (Botkin, 1990). Importantly, however, these equilibrium theories and models can be defined independently of the balance of nature idea and thus, in principle, can be tested.

During the past 20 to 30 years, the ideas of equilibrium and stability usually, but not necessarily, have been considered in relation to each other. An equilibrium point or state usually has referred to a particular system state at which all the factors or processes leading to change are being resisted or balanced. Stability has been defined and used in several ways, but most frequently includes elements of (1) resistance, the capacity of a system to resist an external perturbation, usually measured by the degree to which a variable is changed from its equilibrium value following a perturbation (Innis, 1975; Goodman, 1975; Pimm, 1984); (2) resilience, the rapidity with which a system returns to a previous equilibrium after a perturbation (Innis, 1975; Pimm, 1984; but see Holling, 1973); (3) persistence, the ability of a system to remain within defined limits despite perturbations (Botkin and Sobel, 1975; Pimm, 1984); and (4) variability or constancy, the degree of change or invariance in system properties over a given period of time (Pimm, 1984, 1991). Clearly, use of resistance and resilience as elements of stability presupposes an equilibrium that the system may depart from or return to. Persistence and variability, however, do not necessarily imply

an equilibrium, and their use is not confined to equilibrium theories or models.

Support for the idea of equilibrium in ecological systems often seems to have suggested density-dependent regulative mechanisms, or other forms of internal negative feedback loops. Nicholson (1933) thought that density-dependent mechanisms are pervasive, and hold most populations around an equilibrium. Density-dependent versus density-independent population regulation has been a topic of debate for much of the mid-20th century, and the debate has continued until recently in the context of equilibrium versus nonequilibrium views (Hairston et al., 1960; Ehrlich and Birch, 1967; Caswell, 1978; Berryman, 1987; Reeve, 1988; Godfray and Hassell, 1992). Andrewartha and Birch (1954) challenged the population equilibrium theory, asserting that density-independent effects, which resulted in marked fluctuations for most populations, were generally the rule. Later, Ehrlich and Birch (1967) promoted the idea that populations as well as their environments change constantly, and that the balance of nature idea could be misleading. Levin (1989) asserted that when a system is far from equilibrium, density-dependent factors play a more prominent role in its behavior because of the strong nonlinearity in such a system. Density dependence can serve as the primary mechanism keeping populations within certain bounds, whereas density independence appears to determine system behavior within these bounds; this view is similar to the idea of "density-vague" or liberal population regulation put forward by Strong (1986).

The equilibrium-centered view is also evident in theories for stability in community ecology (Williams, 1964; Slobodkin et al., 1967), in biogeography (MacArthur and Wilson, 1967; also see Wu and Vankat, 1995), and in the early elaboration of ecosystem ecology (Margalef, 1968; Odum, 1969). For example, Patten and Odum (1981) argued that the interplay of biogeochemical cycles and energy flow generates self-organizing feedbacks that give rise to ecosystem order and stability (but see Engelberg and Boyarsky, 1979). Regulation of the transfer of energy and materials represents the principal control mechanism, and ecosystems have evolved certain properties of self-regulation (Loucks, 1986). Similarly, the Gaia hypothesis asserts that the global system is cybernetic, and that "the biota and its environment constitute a single homeostatic system that opposes changes unfavorable for life" (Lovelock, 1987). This Gaian view resembles the supraorganismic conceptualization of the balance of nature, and has become a central concept in what is called "deep ecology" or "eco-philosophy" (Skolimowski, 1988). In addition, the balance of nature idea and the classical equilibrium paradigm have had profound influences on applied ecology, especially on nature conservation, as they have led to the supposition that "nature knows best."

Direct evidence that ecological systems are inherently systems in equilibrium, however, is still lacking. Indeed, individual organisms may be the only systems within which homeostatic mechanisms have been demonstrated to operate. Hall (1988) examined several models of the logistic and Lotka-Volterra types against empirical data that were claimed to support equilibrium predictions. He found, however, that none of the data were actually in agreement with the predictions from the models. Similar results were found by Gilbert (1980) as to the species equilibria projected from the theory of island biogeography, which has had a pervasive influence on ecology and conservation biology (see Wu and Vankat, 1991, 1995 for reviews). Rigorous examination of the "control mechanisms" and "regulation" of material transfers at the ecosystem or higher organizational levels still may be needed if there is yet to be direct validation of the balance-of-nature assumption.

Holling (1973) pointed out that the equilibrium-centered view is virtually static, and cannot account for the commonly observed transient behavior of ecological systems (also see Botkin and Sobel, 1975; Pickett et al., 1992). The classical equilibrium paradigm has usually implied that historical effects, spatial heterogeneity, stochastic factors, and occasional environmental perturbations play a small or negligible role in governing the dynamics of ecological systems, and these systems therefore are reasonably predictable. Numerous studies have demonstrated that history, heterogeneity, stochasticity, and dis-

TABLE 1

A comparison of different perspectives in ecological complexity and stability, indicating criteria
met satisfactorily by the hierarchical patch dynamic paradigm. See text for detailed discussions.

Perspective	"Balance of Nature"	Equilibrium/ static stability	Non-equilibrium/ instability	Multiple equilibria/ homeorhesis	Hierarchical patch dynamics
Information source	Belief, and qualitative data	Theoretical and mathematical	Empirical and mathematical	Mathematical and empirical	Theoretical and empirical
Scope and generality	Broad scope, and general	Broad scope, but specific	Broad scope, but specific	Case-by-case scope	Broad scope; probably general
Extent of testing and outcome	Untestable	Testable only recently, failing	Testable	Relatively untestable	New; testing is preliminary
Application potential	Questionable, dissatisfactory	Generally untenable	Unsatisfactory, limited by scale	Satisfactory, but limited by scope	Satisfactory as a conceptual framework; high potential

turbance all can be very important to the structure and dynamics of ecological systems (e.g., Loucks, 1970, 1985; Holling, 1973; Levin and Paine, 1974; Steele, 1978; Chesson and Case, 1986), and alternative theories and models have been developed to take account of these effects.

In summary, the past several decades have seen something of a paradigm transition, from the balance of nature, to equilibrium/ stability, to nonequilibrium, to multiple equilibria and homeorhesis (Table 1). Hierarchical patch dynamics could be a logical next step. Although the transients in development of the various perspectives in Table 1 cannot (and should not) be separated completely, distinctive attributes for each can be identified to help understand the transition.

NONEQUILIBRIUM AND MULTIPLE EQUILIBRIUM PERSPECTIVES

Several nonequilibrium perspectives have been developed in the search for alternative explanations of ecological phenomena that the equilibrium paradigm clearly fails to account for. Holling (1973) defined "resilience" as a measure of persistence and the ability to absorb change and disturbance within a system. He concluded that the concept of resilience, as he defined it, was theoretically and

practically more appropriate than static stability. On the other hand, Botkin and Sobel (1975) suggested that the concepts of static stability, resistance, and resilience all should be abandoned. They recommended that these terms be replaced with the concept of "Θ-persistence" and a related one, "recurrence." The Θ-persistence is characterized by bounds, as opposed to the static stability used to characterize a single equilibrium. For deterministic properties, an ecological system is Θ-persistent about a state x_0 if $| x_0 - x_t | \leqslant \Theta$ for all $t \geqslant 0$ (i.e., $x_0 - \Theta \leqslant x_t \leqslant x_0 + \Theta$), which means that the system fluctuates between some bounds with x_0 not being a static equilibrium point; for stochastic properties, the Θ-persistence is analogous to an absorbing set in Markov chain theory (Botkin and Sobel, 1975). In essence, this concept of persistence is similar to "resilience" as used by Holling (1973). Based on a review of existing ecological models, DeAngelis et al. (1985) identified three models of stability: stable equilibrium, loose equilibrium (e.g., Botkin and Sobel, 1975), and nonequilibrium models (e.g., Botkin et al., 1972; Caswell, 1978; Huston, 1979). The definition of loose equilibrium resembles that of Θ-persistence. The nonequilibrium models emphasize the openness, transient dynamics, and stochastic processes of ecological systems.

In contrast to the idea of homeostasis or stable stability, the concept of "homeorhesis" (*rhesis* is Greek for "preserving the flow") (Waddington, 1957; O'Neill et al., 1986; Naveh, 1987) or "a dynamic homeorhetic flow equilibrium" (Naveh, 1987) has been suggested. According to this principle, after a perturbation, a system returns to its preperturbation trajectory, or rate of change, instead of returning to some constant equilibrium. Homeorhesis seems to offer a more flexible framework for open systems, one into which nonhomeostasis theories may be incorporated. Because there is empirical evidence that some ecological systems exhibit neither homeostasis nor homeorhesis (O'Neill et al., 1986), this dynamic homeorhetic flow equilibrium view should also be considered an alternative, rather than an exclusive, perspective.

Chesson and Case (1986) defined a nonequilibrium community as one in which "fluctuations or changes in population densities on some spatial scale are an essential part." They identified four types of nonequilibrium community theories. The first type differs from the classical equilibrium theory primarily by the absence of a constant equilibrium; the second type, however, emphasizes fluctuations in density or environmental variables as dominant processes. These two types of theories are distinguished mainly by their assumptions of continuity and discontinuity of density-dependent mechanisms, respectively, and therefore are only enlargements or generalizations of the classical competition theory and its equilibrium extension. Chesson and Case's third type of nonequilibrium community theory emphasizes that the mean of climatic environmental fluctuations does not remain constant over ecological time, and that historical factors play an important role in ecological systems. Their fourth type focuses on the importance of slow, competitive displacement, as well as chance and history, in shaping community structure. The third and fourth types of community theories are free of the equilibrium assumption, and differ fundamentally from the equilibrium-centered stable-community theory.

Nonequilibrium thermodynamics for irreversible processes (Prigogine and Nicolis, 1971; Prigogine, 1978) also has been introduced into ecology as a theoretical basis for explaining stability and instability (O'Neill et al., 1986; Naveh, 1987; Wu, 1991). In this view, ecosystems are seen as dissipative systems, in which a far-from-equilibrium, orderly structure emerges when the interaction between the system and its environment reaches some threshold. When ecosystems constantly absorb energy and material from their environment, entropy (a measure of uncertainty or disorder) decreases and negentropy (a measure of predictability or organization) increases, resulting in a build-up of structural complexity. Thus, the apparent order in the structure and functioning of ecosystems at various scales may arise from the realization of entropy minimization, and can be maintained by a continuous influx of negentropy from the external environment. When a healthy ecosystem is stressed, community respiration may be seen as increasing to "pump out the disorder" through the high entropy production (Odum, 1985), returning to a steady state when a new dissipative structure is formed.

According to the theory of dissipative structure, nonlinear interactions of components and stochasticities can make ecological systems sensitive to small local perturbations, producing consequent fluctuations in behavior. A small random fluctuation can self-amplify, with an increase in entropy production until a new stable state is reached. In other words, fluctuations that imply instability are now triggers or levers for the formation of a new dissipative structure, a phenomenon of order out of disorder. This kind of self-organizing process could result in a hierarchical structure of open systems and the so-called "stratified stability" (O'Neill et al., 1986; Wu, 1991), a concept that is, to some extent, similar to the idea of multiple equilibria or multiple domains of attraction (e.g., Holling, 1973; Levin, 1979).

A multiple-equilibrium perspective in ecology became evident during the 1970s, in large part because of the application of nonlinear mathematics. Nonlinear systems of equations can render multiple periodic orbits and equilibria, each having a basin of attraction (Levin, 1979; Sharma and Dettmann, 1989). Based on diffusion-reaction systems, Levin

(1974, 1976, 1979) elaborated a theoretical basis for explaining the existence of multiple equilibria in spatially structured systems. He argued that spatial patchiness may support alternative locally stable communities, and therefore "overall system pattern is a mosaic of equilibrium patches, each slightly modified by some input from nearby patches" (Levin, 1976). As an alternative to the equilibrium view, the multiple equilibrium perspective has provided satisfactory explanations for a variety of patterns observed in ecological systems, especially with regard to species coexistence and diversity. For example, Holling (1973) discussed a number of empirical examples from aquatic to terrestrial systems that seemed to corroborate the hypothesis of multiple domains of attraction. He asserted that random climatic variations and disturbances, such as fire and pest outbreaks, may drive ecological systems to shift from one equilibrium region to another. More recent experimental and theoretical studies appear to support the idea of multiple equilibria (e. g., Sutherland, 1974; May, 1977; Levin, 1979; Sharma and Dettmann, 1989; Holling, 1992).

Nonlinear systems can exhibit an important threshold phenomenon called bifurcation, in which abrupt, discontinuous changes in system behavior occur as a result of certain parameters crossing an apparent boundary of the domains of attraction (Levin, 1979; Sharma and Dettmann, 1989). The dynamics of these systems seem to be determined primarily around threshold boundaries of great importance. More than 20 years ago, Holling (1973) indicated that the emphasis of research should be on the boundaries of the domains of attraction, rather than on equilibrium states. Since then, a number of studies based on chaos theory and catastrophe theory have focused on threshold phenomena. These have resulted in new perspectives in the dynamics of ecological systems (e.g., May, 1975, 1977, 1986; Schaffer and Kot, 1985; Loehle, 1989; Sugihara and May, 1990). The emergence of chaos theory has made scientists acutely aware of the complex dynamics and unpredictability of nonlinear systems. Various kinds of nonlinearities in pattern and process relationships can make some ecological systems sensitive to small changes in their conditions and thus

inherently less predictable, a view that is ostensibly consistent with the theory of dissipative structure. In addition, chaos theory suggests that determinism does not necessarily increase system stability; rather, it is a condition for the emergence of chaotic behavior. Clearly, these views are in sharp contrast with the predictions of the classical equilibrium paradigm. The implications of chaos theory for ecology seem to be enormous, but are yet to be fully explored (Schaffer and Kot, 1985; Sugihara and May, 1990).

From the above arguments, it follows that much of the disagreement surrounding equilibrium versus nonequilibrium, and stability versus instability, can be attributed to several factors: the ambiguity in various definitions, the different views on effects of spatial pattern, the lack of specification of scale, and differences in theoretical foundations. For example, limit cycles for deterministic systems, domains of attraction in chaotic systems, and constant probability distributions in stochastic models all may be considered as representing some sort of equilibrium or steady state. Ecological systems exist that fluctuate widely (low resistance or low consistency), but still continue to exist (high persistence; see Holling, 1973; Pimm, 1991). Indeed, a balance between resistance and persistence may exist as an evolutionary consequence of the interaction between ecological systems and their fluctuating environments (Holling, 1973). Moreover, it is possible that in multivariable systems, some variables can fluctuate erratically while others seem to be at steady state (Chesson and Case, 1986). It also should be noted that the paucity of sufficiently long time series data and the lack of robust statistical methods may contribute to the controversy over equilibrium versus nonequilibrium views (see Godfray and Hassell, 1992).

It is important to recognize that patchiness is ubiquitous in both terrestrial and aquatic systems, and that ecological processes operate over a wide range of spatial, temporal and organizational scales. Considerations of spatial heterogeneity can fundamentally change one's view of the organization and dynamics of ecological systems (Levin, 1979, 1991). This will be developed further in the sections that follow. One ecologist's "observation window"

may be very different from others. As a result, the same ecological dynamics may be considered transient or in steady state, depending on the scale of observation. To achieve a better understanding of equilibrium versus nonequilibrium properties, or stability and instability of ecological systems, a new conceptual framework is needed that facilitates consideration of heterogeneity and scale, as well as the coupling of structure and function.

HIERARCHICAL PATCH DYNAMICS AS AN EMERGING PARADIGM

As discussed earlier, the attempts to capture the "balance of nature" in equilibrium theory and related concepts have failed for a variety of reasons. Mostly, the failure is due to the lack of recognition of spatial patchiness and the effects of hierarchical linkage across scales in space and time. Such deficiencies lead to difficulties in hypothesis testing, interpretation, and application. Although various nonequilibrium and multiple equilibrium approaches have proven to be valuable, a unifying framework in which these approaches can be integrated is lacking. As a result, neither the classical equilibrium nor the various nonequilibrium views discussed earlier are comprehensive enough to incorporate the effects of patchiness, scale, and hierarchical organization. Still, it is from the study of these effects on the structure and dynamics of ecological systems that some of the most exciting and inspiring ideas have emerged recently.

In this section, we explore the conceptual development and major elements of an emerging paradigm — hierarchical patch dynamics — that provides a framework for explicitly incorporating heterogeneity and scale, and for integrating aspects of equilibrium, nonequilibrium, and multiple equilibrium perspectives. To set the stage, we start with definitions of the concepts of patch and patchiness, and discuss their causes and mechanisms. We then examine the main roots, determinants, and major elements of the new paradigm, giving examples from a variety of empirical and theoretical studies.

PATCHINESS IN ECOLOGICAL SYSTEMS

The importance of spatial patchiness over a wide range of scales in both terrestrial and aquatic systems has been increasingly recog-

nized (Levin and Paine, 1974; Whittaker and Levin, 1977; Steele, 1978; Pickett and White, 1985; Fisher, 1993; Grimm, 1993; Levin et al., 1993; Wu and Levin, 1994). A patch, in its broad sense, refers to a spatial unit differing from its surroundings in nature or appearance (Wiens, 1976; Kotliar and Wiens, 1990). The physical meaning of a patch may vary greatly, depending on the system under study and the scale at which the system is viewed. Other definitions of patch exist, including, for example, a "bounded, connected discontinuity in a homogeneous reference background" (Levin and Paine, 1974); "a region of the environment where the abundance of something, organisms or resource, is high" (Roughgarden, 1977); "a relatively discrete spatial pattern" that may vary in size, internal homogeneity, and discreteness (White and Pickett, 1985); "a spatial concept focused on a small area" as a basic structural and functional unit of the landscape (Forman and Godron, 1986); "a spatial unit that is determined by the organism(s) and problem(s) in question" (Pringle et al., 1988); and "any division or heterogeneity in resources" (Antolin and Addicott, 1991). Thus, on different scales, a patch may be a continent surrounded by oceans, a tract of forest surrounded by agricultural lands and urban areas, a tree gap within a forest, a fire-burned area of bare ground in a plant community, or a plankton aggregate in an aquatic system. Patches can be characterized by their size, shape, content, duration, structural complexity, and boundary characteristics. Thus, spatial patchiness may be defined and quantified in terms of both patch composition (patch types and their relative abundance) and spatial configuration (patch size, shape, juxtaposition, contrast, and boundary characteristics).

Patchiness is both scale- and organism-dependent. Because different species have different abilities for spatial averaging or filtering, heterogeneity in a given environment may have rather different effects on immobile plants versus mobile animals, visual versus nonvisual predators, or, in general, species with distinctive life history characteristics. The scale of patchiness detected by a bird, elk, gopher, or beetle undoubtedly differs. On the other hand, hierarchical spatial structures

can be documented by adjusting the scale of observation (O'Neill et al., 1991; Wu et al., 1994; O'Neill, 1995). Recognition of the scale-dependence and hierarchical structure of patchiness is crucial to understanding the dynamics and stability of ecological systems.

A variety of agents that routinely are considered part of ecological systems can produce patchiness (Levin, 1978; Deutschman et al., 1993). From a population ecological perspective, Wiens (1976) identified several mechanisms that induce environmental patchiness: localized random disturbances (e.g., fire, erosion, tree windfalls), predation, selective herbivory, vegetation patterns, and various combinations of the above. Based on theoretical studies, Roughgarden (1977) discussed five mechanisms: resource distribution, aggregation behavior, competition, reaction-diffusion, and dispersal (also see Levin, 1978, 1992). In the context of landscape ecology, Forman and Godron (1986) classified patches into five types, which are in turn produced by five mechanisms: spot disturbance patches, produced by local perturbations; remnant patches, produced by widespread disturbance; environmental resource patches, produced by heterogeneous distribution of resources; introduced patches from human disturbance; and ephemeral patches due to transient fluctuations in resources.

We propose a conceptual framework of causes of patchiness based on the studies discussed above (Fig. 1). Spatial patchiness includes both physical (or abiotic environmental) and biological aspects, which are interactive and interwoven across spatiotemporal and organizational scales. Biological patchiness occurs at both primary producer and consumer levels. Vegetation patterns present the most conspicuous spatial patchiness and provide a framework for patchiness at consumer levels in terrestrial systems (Wiens, 1976). Different causes and mechanisms operate on different spatial, temporal and organizational scales, and create a hierarchical structure of patchiness. For example, climatic variables (primarily temperature and precipitation) are largely responsible for the spatial pattern in vegetation at the continental or global scale, whereas disturbances such as fires generate patchiness evident from the local stand to landscape scale (Delcourt and Delcourt, 1988; Wickham et al., 1995). Species interactions (e.g., competition, predation) also can induce community-level patchiness (Deutschman et al., 1993). Vegetative propagation can lead to patchiness only on very local scales.

The causes of patchiness may also be considered as proximate vs. ultimate, induced vs. autonomous, and natural vs. anthropogenic across spatial scales (see Deutschman et al., 1993). Holling (1992) identified three categories of processes responsible for the spatial structure of landscapes across scales in time and space: vegetative processes that determine plant growth, plant form, and soil structure at local scales (centimeters to tens of meters in space and days to decades in time); contagious disturbance processes such as fire, insect outbreak, plant disease at mesoscales (hundreds of meters to hundreds of kilometers in space and years to decades in time); and geomorphological processes that dominate the formation of a topographic and soil structure at large scales (hundreds to thousands of kilometers in space and centuries to millennia in time). Recognition of the causes and mechanisms of patchiness in ecological systems, as well as their spatiotemporal domains, is needed to understand their ubiquitousness and complexity.

THE PATCH DYNAMICS PERSPECTIVE

Watt's (1947) Presidential Address to the British Ecological Society, "Pattern and process in the plant community," was considered to be "one of the most influential papers ever published on an ecological subject" (Newman, 1982), and has been generally accepted as the seminal work leading to the current patch dynamics perspective. The "pattern-process hypothesis" presents a view of the community as a dynamic mosaic of patches differing in successional stages. This patch-mosaic-based pattern-process view captures one of the most fundamental characteristics of a wide range of ecological systems, and thus makes both theoretical and methodological generalizations possible (Levin et al., 1993; Wiens et al., 1993; Wu, 1994; Wu and Levin, 1994).

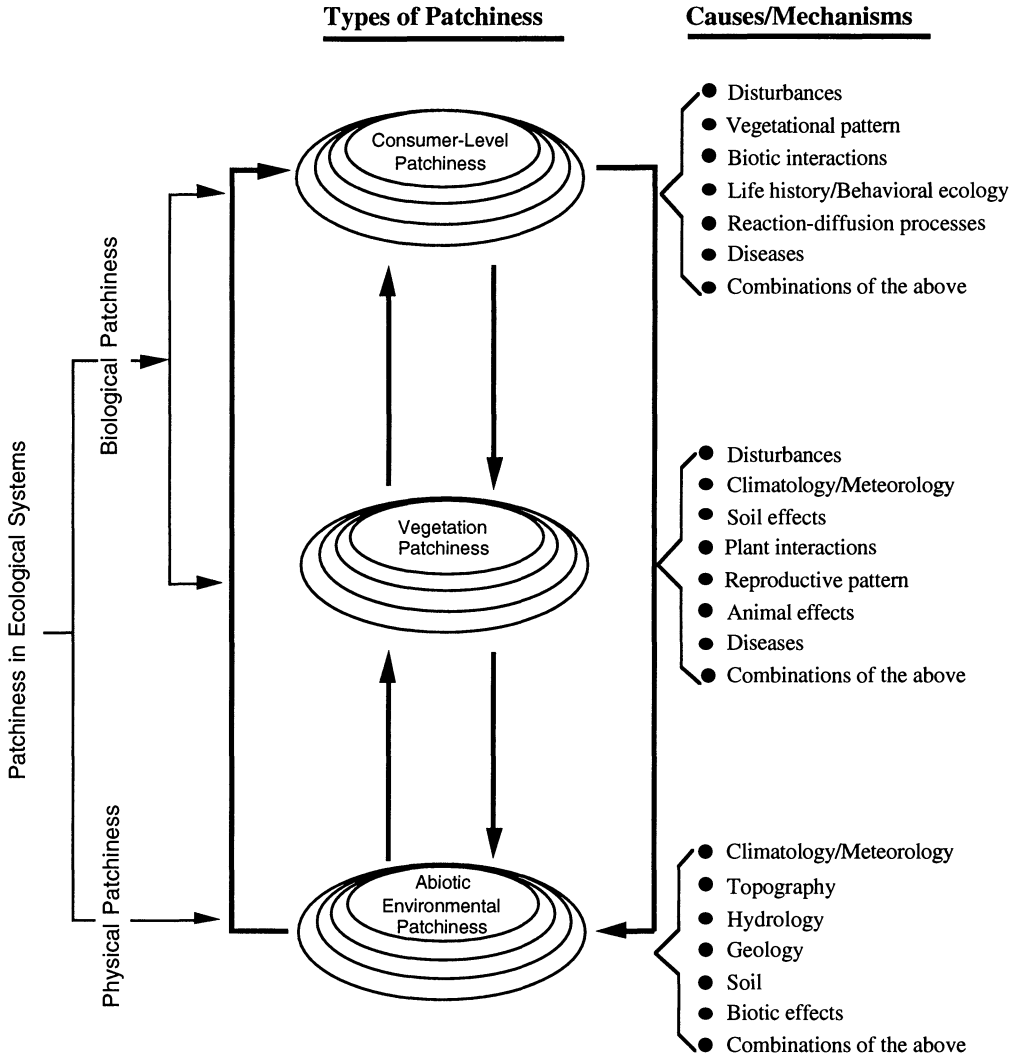**Types of Patchiness** **Causes/Mechanisms**

FIG. 1. A CONCEPTUAL FRAMEWORK OF PATCHINESS AND ITS CAUSES AND MECHANISMS IN ECOLOGICAL SYSTEMS.

Causes and mechanisms can operate at a variety of spatiotemporal and organizational scales, forming different hierarchies. Disturbances may be natural (e.g., fires, windthrows, storms) or anthropogenic (e.g., introduction of exotic species, harvesting of biomass), and these can in turn be divided into finer categories according to spatial and temporal scales. Biological interactions include competition, predation, selective herbivory, parasitism, commensalism, and allelopathy.

Watt's original concept was further developed through a series of empirical and theoretical studies: the intertidal landscape dynamic model (Levin and Paine, 1974; Paine and Levin, 1981), the patch mosaic community concept (Whittaker and Levin, 1977; Steele, 1978), the "minimum dynamic area" concept (Pickett and Thompson, 1978), the "non-equilibrium coexistence" hypothesis (Pickett, 1980), the "shifting mosaic steady state" hypothesis (Bormann and Likens, 1979), the "gap models" of forest succession (Botkin et

al., 1972; Shugart, 1984), the mosaic-cycle concept of ecosystems (Remmert, 1991), and the spatial patch-based modeling approach (Wu and Levin, 1994). As in Watt's original work, most of the above studies have focused on phenomena at the community or ecosystem level.

The patch dynamics approach is complementary to traditional approaches based on organizational levels (e.g., the individual, population, community, and ecosystem). Such organization-level approaches, however, tend to obscure effects of spatial and temporal scales, because the organizational units do not necessarily form a nested hierarchy (Allen and Hoekstra, 1990). A better understanding of ecological and evolutionary processes is facilitated by integrating the two kinds of approaches. In fact, the patch dynamics perspective has been applied to populations, communities, ecosystems, and landscapes equally well, and has become a dominant view in all these areas of ecology (e.g., Pickett and White, 1985; Collins, 1989; Taylor, 1990; Fisher, 1993; Levin et al., 1993; Wu, 1994). For example, most populations occur in patchy systems in which individuals are aggregated, or geographically isolated, into groups or subpopulations. Studies of the structure and dynamics of these patchy systems have led to metapopulation theory (Taylor, 1990; Gilpin and Hanski, 1991; Wu et al., 1993; Hastings and Harrison, 1994). The idea of patch dynamics is also central to the theory and applications of landscape ecology (Forman and Godron, 1986; Wu, 1994; Forman, 1995). While the meaning of a patch varies across scales and biological systems, patch dynamics has been increasingly used as a unifying concept in both marine and terrestrial systems (see Hutchinson, 1953; Steele, 1978; Levin et al., 1993; Wu, 1994).

HIERARCHY THEORY

Hierarchy theory was developed in the framework of general systems theory, mathematics, and philosophy in the 1960s and 1970s (Pattee, 1973; O'Neill et al., 1986; McIntosh 1987). As a theory of complex systems, it has been further developed and applied to overcome old constraints to the progress in ecology and biology (Allen and Starr, 1982;

Salthe, 1985; O'Neill et al., 1986; O'Neill, 1995). Hierarchy theory is related to the theory of dissipative structure in particular and nonequilibrium thermodynamics in general (O'Neill et al., 1986; Wu, 1991). The theory of dissipative structure and the stratified stability hypothesis provide good theoretical bases for understanding hierarchical organization in ecological systems. The dissipative structure concept helps explain how ordered structures emerge hierarchically in open systems, while the stratified stability concept provides a description of how such structures persist and form building blocks for higher levels of organization. For example, the guild is more stable and enduring than its component individual species, and has the potential to serve as a building block for the next higher level of organization (O'Neill et al., 1986). Such a hierarchically organized system can be seen as a system in which levels corresponding with progressively slower behavior are at the top, while those reflecting successively faster behavior are lower in the hierarchy. Higher levels impose constraints on lower levels, and thus can be expressed as constants. On the other hand, the dynamics of the lower levels can be so fast that their signals are smoothed out at higher levels, and often can be treated as averages.

A central tenet of hierarchy theory in ecology is that many complex systems have a structure that is "decomposable," so that both the analysis and understanding of these systems can be enhanced by organizing their numerous components into fewer discrete, interactive units, at levels based on differences in process rates (O'Neill et al., 1986; Phillips, 1995). The methods for performing such a decomposition may vary (Overton, 1975a, b; O'Neill, 1986), but they are by no means arbitrary. Process rates (expressed by, for example, cycle time, response time, or occurrence frequency) are fundamental characteristics of most systems, and thus may serve as a common criterion for decomposing. Other features, such as tangible boundaries and structural components, also can be used. From the theory, discontinuities in hierarchies for organizational, spatial, and temporal scales (e.g., breaks in vegetation pattern, distribution of organism abundance, distribu-

tion of animal body mass, frequency domain of disturbance) are expected to be a common feature of ecological systems (O'Neill, 1988, 1995; Holling, 1992).

Although one does not need to invoke hierarchy theory to realize the importance of scale in studying pattern and process in ecological systems, hierarchical structure provides a strong theoretical basis for explaining the problem of scale and for developing approaches to it. In fact, one of the most significant contributions that hierarchy theory has made up to this point has been to enhance the awareness of scale and facilitate operational measures of scale across a wide range of disciplines (O'Neill, 1995). Recently, hierarchy theory has emerged as a conceptual framework that fosters new approaches to ecological studies, ranging from population regulation to landscape dynamics (e.g., Overton, 1975b; Allen et al., 1984; Pickett et al., 1987, 1989; Urban et al., 1987; Holling, 1992; O'Neill, 1995). While it seems that the patch dynamics perspective has emerged without a clear contribution from or to hierarchy theory (but see Kotliar and Wiens, 1990), we argue in the rest of the paper that the integration of the two has led to what may be called an emerging paradigm with new insights into the complexity and stability of ecological systems.

MAJOR ELEMENTS OF THE HIERARCHICAL PATCH DYNAMICS PARADIGM

As suggested earlier, the hierarchical patch dynamics paradigm has emerged as a result of recent linkage between the patch dynamics perspective and hierarchy theory that emphasizes multiple-scale properties of pattern and process dynamics in ecological systems. In this section, we discuss five major elements of this paradigm.

(1) *Ecological systems as nested, discontinuous hierarchies of patch mosaics.* Ecological systems can be seen as hierarchical systems of patches that differ in size, shape, and successional stage at particular scales. In contrast to traditional approaches in which the individual organism, population, community, or ecosystem is treated as the basic ecological unit of study, the emerging hierarchical patch dynamics paradigm takes a natural spatial unit, the patch, as a fundamental structural and

functional unit. As stated earlier, the patch is scale- and context-dependent. For a given ecological system, patches at different scales can be viewed as forming a nested hierarchy (Kotliar and Wiens 1990; Holling, 1992). An important reason for the existence of patch hierarchies is that disturbances over different spatiotemporal scales (from small to large, short-term to decades long) are common structuring forces for ecological systems (White, 1979; Paine and Levin, 1981; Pickett and White, 1985; Urban et al., 1987; Delcourt and Delcourt, 1988; Pickett et al., 1989).

Let us consider some examples. In a forest, the death of canopy trees creates gaps where the dispersal of seeds, emergence of seedlings, and subsequent differentiation of successional stages take place (Bormann and Likens, 1979; Runkle, 1982). Other disturbance agents (e.g., windthrow, fires, and floods) may create progressively larger patches. As a result, the forest is a hierarchical mosaic system of dynamic patches of different sizes and successional stages. This patch mosaic concept is essential to the gap dynamics theory of forest succession (Botkin et al., 1972; Shugart, 1984), and to the mosaic-cycle concept of ecosystems, in which patches are referred to as "stones" (Remmert, 1991).

An intertidal community is a hierarchical mosaic system of wave-generated, size-varying patches of different successional age (Levin and Paine, 1974; Paine and Levin, 1981). Mounds created by burrowing animals and larger patches by other biotic and abiotic factors (e.g., competition, grazing, soil and topographic heterogeneity such as dune formation, as well as severe fires) form hierarchical systems of patches in grasslands (Loucks et al., 1985; Coffin and Lauenroth, 1989; Wu and Levin, 1994). An aquatic ecosystem also may be viewed as a hierarchical patch mosaic system, with patches being phytoplankton or zooplankton aggregates of different sizes (Steele, 1978). At a broader scale, a landscape is a mosaic of ecosystem patches or land-use types, each of which is in turn a patch hierarchy when examined at a finer scale. Such a hierarchical patch mosaic perspective has been found to be both intellectually and practically effective in the study of spatiotemporal dynamics across a range of

organizational levels (Urban et al., 1987; Delcourt and Delcourt, 1988; Kotliar and Wiens, 1990; Wiens et al., 1993).

Theoretically, the hierarchies of ecological organization (e.g., MacMahon et al., 1978; Woodmansee, 1990) and system processes should lead to similar hierarchies for structural patterns, varying only on discrete scales in space (O'Neill, 1995). This argument has been corroborated by several recent studies. In an extensive analysis of empirical data on the cross-scale structure and dynamics of both aquatic and terrestrial ecological systems, Holling (1992) concluded that "the landscape is hierarchically structured by a small number of structuring processes into a small number of nested levels, each of which has its own physical textures and temporal frequencies." He found that behavioral (e.g., behavioral decisions, or home range) and morphological (e.g., body mass) attributes of animals can be used to identify hierarchical structure and to predict the effects of changes in landscape pattern on community structure. Kolasa (1989) also was able to demonstrate the hierarchical structure of communities in which the distribution of organism abundance is discrete. Importantly, the existence of hierarchical structure within ecological systems can be tested using various spatial pattern analysis methods that have been proven effective in a series of recent studies (e.g., O'Neill et al., 1991; Turner et al., 1991; see also *The pattern-process-scale perspective* section below for examples).

(2) *Dynamics of ecological systems as a composite of patch dynamics.* In hierarchically structured, patchy ecological systems, the phase change of individual patches at local scales and the pattern change in patch mosaics at broader scales together give rise to system dynamics. Thus, the dynamics of ecological systems are composed of the dynamics and interactions of constituent patches on different scales; this is an emergent property in that it is not simply the sum of the individual patch dynamics. The dynamics of a forest, for example, can be seen as a composite that emerges from individual gap dynamics (local processes) and physical and biological interactions with soil and drainage patterns (regional processes). Metapopulation dynamics (to be discussed

in more detail later) describes the composite dynamics of subpopulations and their interactions with large-scale processes (e.g., dispersal or migration). Similarly, the dynamics of a regional landscape is composed of the dynamics of its component ecosystems and the exchanges of energy and materials through topographical, hydrologic, and other physical and biological processes.

In a patch hierarchy, the interconnection between levels, through downward and upward influences, decreases with the number of intervening levels. As a consequence, a better understanding of the dynamics of ecological systems usually is achieved by considering a few (e.g., two) adjacent levels in addition to the focal level (O'Neill, 1988; O'Neill et al., 1989). The focal level is the level at which the phenomenon or process under study characteristically operates. The focal level for studies of energy flow and material cycling, for example, is frequently the ecosystem, whereas the focal level for studying metapopulation dynamics is the landscape. The terms "ecosystem" and "landscape," as used here, do not imply any particular spatial extent, but are defined by the organisms and processes under consideration. The higher level provides a context and imposes top-down constraints on the focal level, and the lower level provides mechanisms and imposes bottom-up constraints. The consequences and significance of the focal level processes can only be understood at the next higher level, whereas the mechanistic explanation as to how the focal level processes operate must be sought at the next level down or, sometimes, at even finer scales (O'Neill, 1988).

(3) *The pattern-process-scale perspective.* The relationship between pattern and process is central to the patch dynamics perspective. A variety of processes can create, maintain, modify, and destroy pattern, and pattern can either facilitate or constrain ecological processes. Examples of ecological processes are numerous: population growth, foraging, dispersal, succession, disturbances, soil formation, and nutrient cycling. These processes are responsible for the formation of patterns, and for determining the dynamics of types of patchiness (Fig. 1). On the other hand, spatial patchiness imposes structural constraints on

ecological processes operating at different organizational levels. Thus, one should study ecological processes in their context and search for patterns based on underlying processes.

Pattern and process operate on a wide range of scales, and their characteristics are clearly associated with scale (Allen et al., 1984; Delcourt and Delcourt, 1988; Levin, 1992; Wessman, 1992; Fisher, 1993; Wu, 1994). Pattern, be it spatial, temporal or functional, is inseparable from scale in theory and practice. The choice of scale can behave like a blinder, a filter, or a magnifier, depending on the appropriateness of the observation window size (Allen and Starr, 1982; O'Neill et al., 1986). Thus, scale affects pattern to be observed, and ought to be an integral part of search for pattern. Several authors have shown that descriptors of spatial pattern (e.g., autocorrelation measures, variance, contagion, and dominance) may change considerably with scale (e.g., Turner et al., 1989; O'Neill et al., 1991; Wu et al., 1994; Qi and Wu, 1995). A number of analyses using such methods have shown "breaking points," that mark the boundaries of the "domains of scale" (Milne, 1988; Wiens, 1989; Wiens and Milne, 1989). For example, although fractal dimension changes with spatial scale in general, it may remain constant within certain ranges of scale where self-similarity exists. Similarly, spatial variance can exhibit a staircase-like (or stepwise) pattern of change when obtained over a wide range of scales (O'Neill et al., 1991; O'Neill, 1995). Because of the scale dependence of the pattern being measured, results of pattern analysis need to be presented with explicit specification of the scale at which the data have been obtained. Moreover, pattern analysis over multiple scales seems preferable whenever feasible (Wiens, 1989; Wiens and Milne, 1989; Wu et al., 1994; Qi and Wu, 1995).

Ecological processes and environmental controls also shift with scale along a patch hierarchy. For example, leaf photosynthesis is central to the growth of an individual plant and is primarily determined by the physiology of the species and micrometeorological conditions, whereas biogeochemical cycling and climatic variables become dominant in controlling ecosystem productivity at the stand or landscape levels. Species diversity may be significantly influenced by resource heterogeneity and biological interactions (e.g., competition and predation) at local scales, but it is highly correlated with evaportranspiration at regional and continental scales, suggesting rather different controlling processes and environmental factors (see Wickham et al., 1995 for a review).

Importantly, the domains of scale or characteristic scales detected by pattern analysis methods usually signify different underlying processes. Several recent studies have demonstrated that inferring processes from pattern analysis across a range of scales is possible (see O'Neill et al., 1991; Levin, 1992; O'Neill, 1995). One of the most important aspects of identifying the domains of scale through detecting spatial pattern is to facilitate the translation or extrapolation of information across scales. Although a functional representation of an ecological relationship may be distorted when translated across scales owing to "spatial transmutation" (O'Neill, 1979; King et al., 1991; Wu and Levin, 1994), linear or near-linear extrapolation should be expected within a given domain of scale over which similar processes are functioning (Wiens, 1989; Wiens and Milne, 1989).

The pattern-process-scale perspective clearly has moved to a position of prominence in current ecological thought and in earth sciences in general (see di Castri and Hadley, 1988; DeBoer, 1992; Levin, 1992). Recent studies have demonstrated the usefulness of this perspective in several fields, including metapopulation dynamics (Gilpin and Hanski, 1991; Wiens et al., 1993; Wu and Levin, 1994), vegetation dynamics (Bormann and Likens, 1979; Pickett et al., 1987), freshwater ecology (Fisher, 1993; Grimm, 1993), ecosystem structure and functioning (Holling, 1992), landscape dynamics (Wiens and Milne, 1989; Turner et al., 1993), soil science (Burrough, 1983), and biogeomorphology (DeBoer, 1992; Phillips, 1995).

(4) *The nonequilibrium perspective.* As opposed to the classical equilibrium viewpoint, a hierarchical patch dynamics paradigm permits emphasis on nonequilibrium and stochastic processes as elements of what was known previously as ecological stability (or balance in nature). In particular, ecological systems at

small spatial scales can be treated as exhibiting continuous transient dynamics, that is, as ephemeral systems with no equilibrium properties. Equilibrium theories and models are usually not valid at such small spatial scales (DeAngelis and Waterhouse, 1987; Wu and Levin, 1994). Abiotic and biotic disturbances often introduce the local transient dynamics into ecological systems (Pickett and Thompson, 1978; Pickett, 1980; Paine and Levin, 1981; Loucks et al., 1985). Indeed, patch dynamics, in a narrow sense, has been used to convey the idea of nonequilibrium conditions or instability (e.g., Pickett and Thompson, 1978; Pickett and White, 1985). Ecological systems exhibit nonequilibrium dynamics not only on small scales where stochasticities usually dominate, but also on very large scales where long-term processes leading to geological, climatological and evolutionary changes come into play. Thus, scale clearly affects what will be seen as nonequilibrium, transient, or unstable dynamics.

(5) *Incorporation and metastability.* Two further, but interrelated components of the hierarchical patch dynamics paradigm are the principle of incorporation and the concept of metastability, both of which are related to hierarchy theory and nonequilibrium thermodynamics. As already noted, lower-level processes are an integral part of higher-level structure and processes in a hierarchical system (O'Neill et al., 1986; O'Neill, 1988). Because of this, nonequilibrium patch processes at one level often translate to a quasi-equilibrium state at a higher level. This homeorhetic, quasi-equilibrium state has been termed metastability (Naveh, 1987; O'Neill et al., 1989). It illustrates the conceptualization of order out of apparently random fluctuation, where nonequilibrium dynamics at one scale can become the means of quasi-equilibrium at a higher level (either spatially larger or temporally longer). For example, single treefalls induce local gap dynamics that create nonequilibrium outcomes at the gap level; however, gaps are incorporated readily as an area-wide mean process at a larger forest stand level, leading to a "shifting mosaic steady state" (Watt, 1947; Bormann and Likens, 1979). A large blowdown cannot be incorporated in forest stand dynamics, but it can be at a landscape of larger scale (Urban et al., 1987). By the same token, wildfires may be incorporated by a larger regional landscape. The decrease in variation with increasing spatial scale can be used to demonstrate quantitatively this incorporation principle (e.g., Levin and Buttel, 1986; O'Neill et al., 1991; O'Neill, 1995).

The experimental and theoretical work by Levin and Paine (1974; and Paine and Levin, 1981) also illustrates the principle of incorporation. Concerned with the spatial and temporal patterns of a rocky intertidal system, they found that the steady state dynamics at the landscape level was composed of transient dynamics at the patch level. Loucks (1970) presented an example of incorporation in the time domain through the "wave-form dynamics" hypothesis. He found that, in the southern Wisconsin forests, the long-term steady state was composed of a series of transient responses triggered by random perturbations (fires) with intervals of 30 to 200 years. Forest fires were viewed as destabilizing on a short-term scale, but stabilizing on a long-term scale. Also, Rahel (1990) found that some communities (e.g., phytoplankton assemblages) appear to fluctuate at short time scales but are more stable when viewed over a longer period of time. In nutrient cycling, fluctuations in nutrient supply are incorporated by temporal mechanisms through functional components that take up, retain (over a wide range of time-spans), and recycle nutrients (O'Neill et al., 1986).

Both incorporation and metastability are dependent on the types of processes (e.g., disturbances) and their spatiotemporal scales in the system under consideration. Our ability to understand and predict the dynamics of ecological systems, however, will be greatly enhanced by improvements in the quantification of these concepts. Recently, Turner et al. (1993) presented an interesting model that considers disturbance in terms of its relative temporal and spatial scale, i.e., the ratio of disturbance interval to recovery time (T), and the ratio of the extent of disturbance to the size of the landscape (S). The modeled landscape was a square grid with 100×100 cells, in which randomly distributed disturbance with fixed T and S gave rise to a dynamic

vegetation mosaic with eight seral stages. Through a factorial simulation experiment, the authors were able to generate a "state-space diagram" which they used to define domains of landscape stability. Based on the simulation results, they concluded that landscape systems could exhibit different kinds of dynamics, ranging from equilibrium or steady state with little fluctuation, to stable with low, high and very high variance, to unstable with bifurcation or even crash characteristics. Turner et al. (1993) has demonstrated a way to quantify the concepts of incorporation and metastability by focusing on the relative scale of disturbance in time and in space. Using such a modeling approach, others will be able to examine whether a specific disturbance can be incorporated by a given landscape, or whether a landscape is stable, given one or more disturbances operating on some known spatial and temporal scale. Several patch dynamics modeling approaches to be discussed in the next section also serve as quantitative approaches for insights into these elements of the hierarchical patch dynamics paradigm.

PATCH DYNAMICS MODELING

It is evident from the previous sections that recent studies are showing increasing sophistication in two aspects of the balance of nature: the ideas of equilibrium, and stability or instability. We have seen the assumption of equilibrium relaxed or abandoned, and the hierarchical context has become more explicit. Modeling, as a formalized expression of what has hitherto been descriptive and conceptual, can be an indispensable means for expressing patch dynamics hierarchically and making description an operational reality. In particular, recent developments in hierarchical patch dynamics modeling hold the prospect of linking pattern and process formally, relating local dynamics to larger scale phenomena, and integrating information across levels in ecological systems (e.g., Reynolds et al., 1993; Vasconcelos et al., 1993; Wiens et al., 1993; Wu and Levin, 1994). Such formalization, however, still presents both ecological and mathematical challenges. In this section, we discuss the modeling approaches that could serve as points of departure.

Several types of patch dynamic models have been developed. They include island biogeographic models, patch-occupancy models, diffusion-reaction patch models, neighborhood models, quasi-spatial patch demographic models, raster-based (or grid-based) spatial patch models, and vector-based (or patch-based) patch models. These modeling approaches have been developed and used, with various mathematical roots, in areas such as population ecology, metapopulation dynamics, community ecology, biogeography, and landscape ecology. The theory of island biogeography (MacArthur and Wilson, 1967; Wu and Vankat, 1991, 1995) provided probably the first formal structure to relate spatial pattern to ecological processes. Although an assumption of equilibrium is central to the theory, the idea that the dynamics of patches are determined by processes with spatial variability has inspired other models dealing with patchy environments. Indeed, the heuristic value and influence of the theory can be found in many patch models, from population dynamics to landscape ecology (e.g., Levin, 1976, 1978; DeAngelis et al., 1979; Gilpin and Hanski, 1991; Wu, 1994; Wu and Vankat, 1991, 1995).

Patch-occupancy models usually assume a large number of fairly similar patches in the system under study, and state variables are usually the proportions of patches occupied and unoccupied by populations or by different species. This approach was introduced by Levins (1969), and represents one of the first dealing with spatial patchiness. It has been used widely to study single-species population dynamics as well as multi-species interactions, and has formed a cornerstone for metapopulation theory (see Gilpin and Hanski, 1991; Hastings and Harrison, 1994 for recent reviews).

Another frequently used mathematical framework for patch dynamics modeling is of the form

$$\frac{dY_i^u}{dt} = f_i^u(Y^u, X^u)$$

+ (net exchange with other patches)
+ (net exchange with matrix),   (1)

where Y^u is the vector $(Y_1^u, Y_2^u, \ldots, Y_n^u)$ of

state variables for a given patch u, X^u is the vector $(X_1^u, X_2^u, \ldots, X_n^u)$ of parameters accounting for the same patch, and f^u is the specific functional relationship (Levin, 1976). The degree of detail incorporated in specific models may vary greatly, and these models generally may be categorized as diffusion-reaction models (e.g., DeAngelis et al., 1979; Okubo, 1980; Wiens et al., 1993; Wu et al., 1993).

While diffusion-reaction models have been applied mainly to animal populations, neighborhood models have been developed to study plant growth and population dynamics (e.g., Pacala and Silander, 1985; Wu et al., 1985). Neighborhood models are based on the assumptions of sessility of plants, localized interactions among individuals, and resource-plant growth relationships. A neighborhood is usually defined as a circular area centered on a focal individual plant, where other individuals are encountered and compete for space and resources. New insights into interactions among resource heterogeneity, species competition, and the structure and dynamics of plant populations and communities can be gained by integrating models of this sort with field experiments. Neighborhood models seem to be effective and accurate in studying plant-plant interactions at relatively small scales (e.g., local communities or smaller), but applying such approaches at very large scales (e.g., regional landscapes or larger) is rather difficult, if possible at all, without significant simplification in model structure. Also, the conceptualizations involved in these modeling approaches make their application to most animal populations very difficult.

Levin and Paine (1974; Paine and Levin, 1981) first formulated a patch demographic model to predict the distribution pattern of an age- and size-structured patch population in an intertidal landscape. The approach, a nonequilibrium island biogeographic construct, differs importantly from the diffusion-reaction approach. The Levin-Paine patch demographic model considered the distributions of the age and size of patches in the form

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial \alpha} + \frac{\partial}{\partial \xi}(g\rho) = -\mu(t,\alpha,\xi)\rho \quad (2)$$

where $\rho(t,\alpha,\xi)$ is the probability density function describing the frequency distribution of patches of age α and size ξ at time t, $\mu(t,\alpha,\xi)$ is the mean extinction rate of patches of age α and size ξ at time t (due to intrapatch succession), and $g(t,\alpha,\xi)$ is the mean growth rate of patches of age α and size ξ at time t (due to patch shrinkage or expansion). Therefore, the number of patches with size between ξ_1 and ξ_2 and age between α_1 and α_2 at any point in time can be obtained by integrating (Levin and Paine, 1974),

$$N_p(t,\xi_1,\xi_2,\alpha_1,\alpha_2) = \int_{\alpha_1}^{\alpha_2}\int_{\xi_1}^{\xi_2}\rho(t,\alpha,\xi)d\xi d\alpha. \quad (3)$$

Population density or other biological variables of interest may be coupled with the patch demographic model in the following general form (Levin, 1976):

$$\bar{n}_j(t) = \frac{1}{A(t)}\left\{\left[A(t) - \int_0^\infty\int_0^\infty \xi\rho(t,\alpha,\xi)d\alpha d\xi\right]\varphi_j^0(t) \right.$$
$$\left. + \int_0^\infty\int_0^\infty \xi\rho(t,\alpha,\xi)\varphi_j(t,\alpha,\xi)d\alpha d\xi\right\} \quad (4)$$

where $\bar{n}_j(t)$ is the overall population density for species j over the landscape, $\rho(t,\alpha,\xi)$ is the probability density function that describes the frequency distribution of patches of type α and size ξ at time t, $\varphi_j(t,\alpha,\xi)$ is the population density of species j within a patch of type α and size ξ at time t, $\varphi_j^0(t)$ is the population density of the same species in the nonpatch area, and $A(t)$ is the total area of consideration at time t.

The patch demographic formulation also was successfully applied to modeling forest gap dynamics (Runkle, 1982). Clark (1991) and Kohyama (1993) developed quasi-spatial patch models to couple disturbance patch demography with tree species population dynamics and net primary productivity on shifting mosaic landscapes.

All these patch dynamic modeling approaches have been useful, on either a theoretical or an empirical basis, in dealing with the effects of spatial patchiness and scale on the observable structure and dynamics of ecological systems. Still lacking, however, is a mathematical framework incorporating the complexity from spatiotemporal heterogeneity and the hierarchical structure of more than

two levels. To deal effectively with the problems of spatial and temporal patchiness, scale, and hierarchical structure, spatially explicit simulation modeling seems to be almost the only approach available. A group of quasi-spatial patch dynamic simulation models (gap models) has been used for some applications (see Shugart, 1984 for a review). More recently, other gap models have been adapted in spatially explicit terms for forests (e.g., Smith and Urban, 1988; Wissel, 1991) and grassland ecosystems (e.g., Coffin and Lauenroth, 1989). These models take a grid-based approach in which patches are considered as single grid cells or aggregates of multiple cells within a regularly divided grid. The potential exists for spatial and scale effects and hierarchical structure to be incorporated. This approach has advantages, and is effective in modeling certain ecological processes, but it may be inadequate and impractical in cases where overlapping among patches seriously affects the dynamics of the system under study.

Recently, Wu and Levin (1994) developed a spatially explicit patch-based model of the dynamics of pattern and process in a grassland system. It treats patches as individual objects changing in shape, size, age, and composition, and accounts explicitly for overlaps among patches. The model has two main modules: a spatially explicit patch demographic module and a spatially explicit, patch-based population dynamic module. The parallel formulation of the patch population model and an embedded species population model enables scrutiny of the dynamics and spatial patterns of both patches and plant populations. The formulation also makes the modeling approach suitable for studying a range of problems, such as population dynamics in a fragmented environment where patches are habitats, or plant-parasite and plant-insect interactions where patches are individual plants. Although the current version of the model (PatchMod) considers only two hierarchical levels explicitly, the approach readily allows addition of more processes at other hierarchical levels. Because the spatial and temporal dynamics of heterogeneous systems with complex hierarchical properties can be modeled in spatially explicit simulation approaches (raster-based and vector-based), these hold much potential for developing and testing the emerging hierarchical patch dynamics paradigm.

Other modeling methodologies and techniques may enhance the development of hierarchical patch dynamic models. For example, a hierarchical modeling approach, the "FLEX paradigm" developed by Overton (1975b), and successfully applied to forest and lotic ecosystems (Overton, 1975b; McIntire and Colby, 1978), will find greater use as the hierarchical patch dynamics paradigm develops. Recently, several different strategies have been proposed for extrapolating information across hierarchical levels and domains of scale (e.g., Iwasa et al., 1987, 1989; King, 1991; Rastetter et al., 1992; Reynolds et al., 1993). In particular, Reynolds et al. (1993) proposed a "three-level-chain" hierarchical scheme that appears to be highly sensible for modeling complex systems over broad scales. With this approach, a series of models is built along the organizational hierarchy and across a range of scales where ecological processes and their controls operate. Each model is a three-level construct in that it is built around a focal level, with the constraints from the adjacent upper level and mechanistic information from the next lower level being considered. Upscale extrapolation is done by taking outputs from one model as inputs into another at the next higher level.

A recent breakthrough in computer simulation, which has significant implications for hierarchical patch dynamic modeling, is the development of object-oriented programming (OOP). The OOP approach is "a method of implementation in which programs are organized as cooperative collections of objects, each of which represents an instance of some class, and whose classes are all members of a hierarchy of classes united via inheritance relationships" (Booch, 1991). Such a method has inherent advantages for modeling spatial and temporal processes simultaneously on multiple scales. Recent ecological applications seem to suggest that this hierarchical, modular simulation approach may have much to offer for advancing hierarchical patch dynamics modeling (e.g., Vasconcelos et al., 1993).
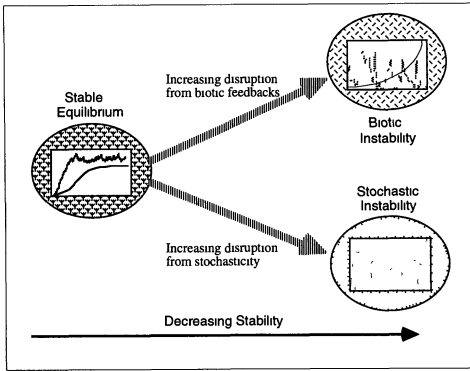
FIG. 2. SCHEMATIC REPRESENTATION OF ECO-
LOGICAL SYSTEMS IN A SCALE FROM STA-
BLE TO UNSTABLE (MODIFIED FROM
DEANGELIS AND WATERHOUSE, 1987).

INSTABILITY AND STABILITY OF ECOLOGICAL SYSTEMS

Given that nonequilibrium patch dynamics can be a common phenomenon at a range of scales, how do ecological systems manage to persist in the presence of destabilizing forces? Since the equilibrium and stability viewpoints are not able to provide full explanations for ecological persistence, what does the hierarchical patch dynamics paradigm have to offer?

Before we can address the above questions effectively, it will be necessary to explore more fully the mechanisms available for integrating and stabilizing ecological systems. Wiens (1984) has asserted that ecological systems exist along a spectrum from stable equilibrium (controlled primarily by self-regulating biotic forces such as population regulation) to nonequilibrium systems (dominated by stochasticity). DeAngelis and Waterhouse (1987) extended the spectrum to include two types of potentially destabilizing forces in ecological systems: biological instability caused by strong nonlinear biological feedbacks and time-lags, and stochastic instability caused by demographic haphazardness and environmental fluctuations (Fig. 2). Accordingly, they distinguished three general categories of ecological communities: (1) "stably interactive communities" that are dominated by negative feedbacks and have one or more apparent stable equilibria, (2) "unstably interactive communities" that may be dominated by positive feedbacks and have one or more unstable equilibria, and (3) "weakly interactive communities" that are dominated by stochastic fluctuations and have no equilibrium (Fig. 2). A system, be it a patch ecosystem or a patch mosaic, can exhibit nonequilibrium dynamics when strong biotic interactions result in the dominance of destabilizing positive feedbacks over stabilizing negative feedbacks, or when negative biological feedbacks are over-whelmed by stochasticity. Although this classification obviously is focused at the community level, it also can be applied to other levels of ecological systems or patch mosaics at various spatiotemporal scales.

The description by DeAngelis and Waterhouse (1987) as to types of instability is supported by both theoretical and empirical studies. For example, a wide range of fluctuations, and even chaotic dynamics, can be produced when strong biotic interactions (nonlinear feedbacks) are introduced into simple deterministic models such as first-order difference equations of the logistic or Lotka-Volterra type (May, 1975, 1986). Empirical studies as well, although scarce, appear to support the idea of biotic instability in certain population and epidemiological systems (Schaffer and Kot, 1985; Sugihara and May, 1990; Tilman and Wedin, 1991). In practice, it is difficult to distinguish between biotic instability and stochastic fluctuations because, remarkably, the system-level consequences of the extremes of density-dependence and density-independence seem much alike (see May, 1986). New techniques are being developed to address this problem (Sugihara and May, 1990), however. The destabilizing effects of demographic and environmental stochasticities on ecological systems, from the population to the ecosystem level, have all been documented in both empirical and theoretical studies (e.g., May, 1986; Soulé, 1987).

How do ecological systems cope with instabilities and persist? Expanding on the work of DeAngelis and Waterhouse (1987) and others (e.g., den Boer, 1968; Loucks, 1970; O'Neill et al., 1986; Levin, 1992; Wu and Levin,

1994), the following sections explore several theoretical stabilizing mechanisms that could exist in ecological systems and that are consistent with the hierarchical patch dynamics paradigm.

(1) *Spatial incorporation of localized biotic feedback instability* (mechanism A in DeAngelis and Waterhouse, 1987). When an ecological system is composed of patches that are only weakly or occasionally coupled, spatial quasi-isolation and asynchronous dynamics of patches may achieve system-level metastability by dissipating biotic feedback instability at the individual patch level. This is essentially a result of the interplay between biological processes and spatial patchiness at multiple scales. A few theoretical investigations based on host-parasitoid and predator-prey models have shown that spatial subdivision and migration do not seem to improve system persistence in the absence of density-dependent coupling (see Reeve, 1988). Apparently, asynchrony among component patches could damp system-level fluctuations just for statistical reasons. Conceptually, this mechanism resembles somewhat the concept of "the spreading of risk" (see below), but it still awaits evaluation against empirical data.

(2) *Environmental disturbance control of biotic feedback instability* (mechanism B in DeAngelis and Waterhouse, 1987). Stochastic environmental disturbances may prevent biotic feedback instabilities from eliminating ecological systems, thus resulting in system-level metastability (Loucks, 1970; Bormann and Likens, 1979; Pickett, 1980). Frequent disturbances can keep biotically unstable populations within some bounds, and may effectively prevent species exclusions resulting from intense competition or prey overexploitation (e.g., Hutchinson, 1961; Huston, 1979; Chesson, 1981; Wu and Levin, 1994). The environmental disturbance control mechanism in ecological systems also has been discussed previously in terms of the regeneration niche (Grubb, 1977).

(3) *Biotic compensatory control of stochastic instability* (mechanism C in DeAngelis and Waterhouse, 1987). Biotic compensatory forces may prevent what appear as stochastically dominated ecological systems from disappearing

due to strong negative feedback effects at low levels in the hierarchical linkages. In other words, the probability of extinction for ecological systems that fluctuate dramatically due to unpredictable forces may be reduced significantly through certain mechanisms involving adaptation and life history characteristics of organisms in these systems. Such phenomena include transient dynamic populations living in a community with a small number of secure habitat patches, or populations whose rates of reproduction increase at low densities (e.g., Connell and Sousa, 1983; Connell et al., 1984).

(4) *Spatial incorporation of stochastic instability* (mechanism D in DeAngelis and Waterhouse, 1987). Asynchronous environmental disturbances also can serve as a mechanism for the persistence of stochastically determined patches that are spatially isolated within a system interacting at a higher hierarchical level. In this case, the disturbances operate at spatial scales smaller than those of the ecological system under consideration. For example, locally unstable populations may persist at a community or landscape level because of frequent colonization from disturbance-free patches (e.g., Levin, 1974; Runkle, 1982; Wu and Levin, 1994). This phenomenon has been termed "the spreading of risk" (den Boer, 1968). The outcome observed can be thought of as an interplay between spatial patchiness and hierarchical structure of ecological systems.

(5) *Absorption of ecological instability through heterogeneity.* Heterogeneity here refers to redundancy in system functions and in the pattern by which they are distributed (O'Neill and Reichle, 1980) as well as habitat diversity. Spatial patchiness in both physical and biological environments also may provide a mechanism for persistence of ecological systems (see Steele, 1978; Levin et al., 1993). Numerous studies of species-area relationships have shown that habitat diversity usually contributes to species diversity and persistence (e.g., Williams, 1964; Boecklen, 1986). Spatially heterogeneous biotic factors, such as predation rate, may also permit species in direct competition to coexist in the same community even with uniformly distributed re-

sources (Levin, 1976). Redundancy in function and pattern could be viewed as essential to the persistence of ecological systems because they both minimize the probability of a complete loss in performance of critical functions (O'Neill and Reichle, 1980).

The above analysis of stabilizing mechanisms provides a basis for understanding ecological metastability, possibly the closest technical equivalent to "balance of nature." Different combinations of two or more of these mechanisms can be expected to operate in real ecological systems at different spatial, temporal and organizational scales. From the previous discussion, we can see that stabilizing and destabilizing factors can interact and may even convert to one another. Quantitative expressions for many of the mechanisms discussed above are still only in a preliminary stage and need further field testing. A comprehensive perspective is also clearly needed to perceive how the different mechanisms operate in nature. The most important contribution from the hierarchical patch dynamics paradigm toward understanding ecological stability (or instability) probably lies in the framework it provides for studying how spatiotemporal heterogeneity, scale, and hierarchical organization influence the structure and dynamics of ecological systems. The "rules of the game" for ecological system stability can change drastically across scales of time, space, and organization. Thus, the predictability of ecological systems also may depend on scale, as well as the nature of the pattern and processes under consideration.

DISCUSSION AND CONCLUSIONS

We have seen that the balance of nature concept implied a constant (and perhaps desirable) equilibrium and static stability that was later to characterize the classical equilibrium paradigm in ecology. The idea of "balance" has had a cultural and religious connotation rather than a strict scientific foundation, and even its heuristic role may be misleading. The concepts of point equilibrium, static stability and homeostasis also are misleading for general use in ecology. Theories are needed that take into account the effects of temporal and spatial scale and heterogeneity on ecological processes. Equilibrium models in ecology, al-

though often echoing the balance of nature, have roots in mathematics and physics and are testable in principle. However, the classic equilibrium theory rests on models of logistic and Lotka-Volterra types that generally neglect spatial patchiness (Caswell and Etter, 1993); it often fails to explain the dynamics or stability of ecological systems.

A fundamental flaw in the classical equilibrium view lies in its inability, in most applications, to incorporate spatial heterogeneity and multiplicity in scale when an apparent stability of ecological systems is observed. With equilibrium redefined as some bounded range, and with ecological systems placed in their hierarchical context, equilibrium theories may remain useful for describing persistence or metastability of ecological systems. However, the spatial, temporal and organizational scales need to be explicitly linked, as models based on small-scale processes are incorporated at larger scales with appropriate criteria and parameters for those scales (O'Neill, 1988; Wu and Levin, 1994; Phillips, 1995). When large-scale perturbations such as habitat fragmentation and global climatic changes are considered, one appreciates more clearly the need to understand what potential equilibrium patterns may be observed over very long time-spans and at large spatial scales.

With new developments in the fields of metapopulation dynamics, landscape ecology, conservation biology, and global change, the hierarchical patch dynamics paradigm may be seen as a way of unifying equilibrium and nonequilibrium perspectives across multiple scales of space and time. The shift in perspective is evidenced in the transition from concern with equilibrium, homogeneity, determinism, and local or single-level phenomena, to nonequilibrium, heterogeneity, stochasticity, and hierarchical properties of ecological systems. The major elements of the emerging hierarchical patch dynamics paradigm include conceptualizing ecological systems as nested hierarchies of patch mosaics, viewing the dynamics as the outcome of composite patch dynamics, the pattern-process-scale perspective, the nonequilibrium perspective, the principle of incorporation, and the idea of metastability. Modeling of patch dynamics is crucial to relating pattern and

process, and in scaling and understanding stability in ecological dynamics when studied across hierarchical levels. The quantitative approaches now available or under development for patch dynamics offer the prospect of explicit consideration of "emergent properties" when applied to hierarchically linked systems. Hierarchical patch dynamics represents an approach that links otherwise disparate phenomena, and helps to formalize testable new hypotheses and theories.

Nature is not in constant balance, and patchiness is ubiquitous. The metastability suggested by hierarchical patch dynamics differs theoretically and structurally from the static stability implied by both the balance of nature and the classical equilibrium paradigm. Ecological stability is scale-dependent. Metastability is dependent on the presence of and interaction among spatial, temporal and organizational scales. Metastability or persistence for many ecological systems is usually found at the meta-scale, in contrast to the transient dynamics that have been used to characterized local and large scale phenomena. Harmony is embedded in the patterns of fluctuation, and ecological persistence is "order within disorder."

The hierarchical patch dynamics paradigm represents a robust theoretical framework for coupling pattern with process at different scales, and for facilitating, operationally, a unification of concepts and approaches among different types of ecological systems (Steele, 1985; Levin et al., 1993; Wu, 1994). For example, metapopulation theory, landscape ecology and conservation biology all attempt to deal with biological entities and processes functioning within patchy environments. Studies of the dynamics of subpopulations, the interactions among landscape elements, and the analysis of population viability or species persistence should take into account factors and processes operating at these different scales (Noss, 1990; Wiens et al., 1993; Wu, 1994). A hierarchical patch dynamics perspective can serve as a common ground on which the three can be united (Wu, 1994).

The emerging paradigm also holds practical implications for applied ecology. Hierarchical patch dynamics emphasizes, rather than avoids, the importance of disturbances, heter-ogeneity, and multiple spatiotemporal scales in managing or conserving ecological systems. Consider, for example, that observed differences in process rates suggest that small-scale events induce dynamic responses, usually at a high frequency, while at large scales these dynamics are at a low frequency. As a result, small ecological systems are generally subject to higher risks of extinction from either biotic feedbacks or stochastic instabilities than are large systems. By explicitly recognizing the importance of pattern-process interactions and scale, the hierarchical patch dynamics paradigm also helps to link biological processes with their context, e.g., to maintain ecosystem processes and landscape structure while conserving species.

A further implication lies in improving our means of understanding change and dealing with that change when necessary. Although the environmentalism of the 1960s and 1970s may not have generated solutions to problems, perhaps partially because of a belief in the balance of nature, failure to understand naturally and anthropogenically induced disturbances can lead to destructive, unintended ecological consequences (Botkin, 1990; Pickett et al., 1992; Wu, 1992). Almost 70 years ago, Aldo Leopold (1927) pointed out that "the balance of nature in any strict sense has been upset long ago. . . . The only option we have is to create a new balance objectively determined for each area in accordance with the intended use of that area." By taking a positive approach, by improving our understanding of how nature works, and managing it accordingly, we are more likely to sustain a livable environment, and achieve harmony between humanity and nature.

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