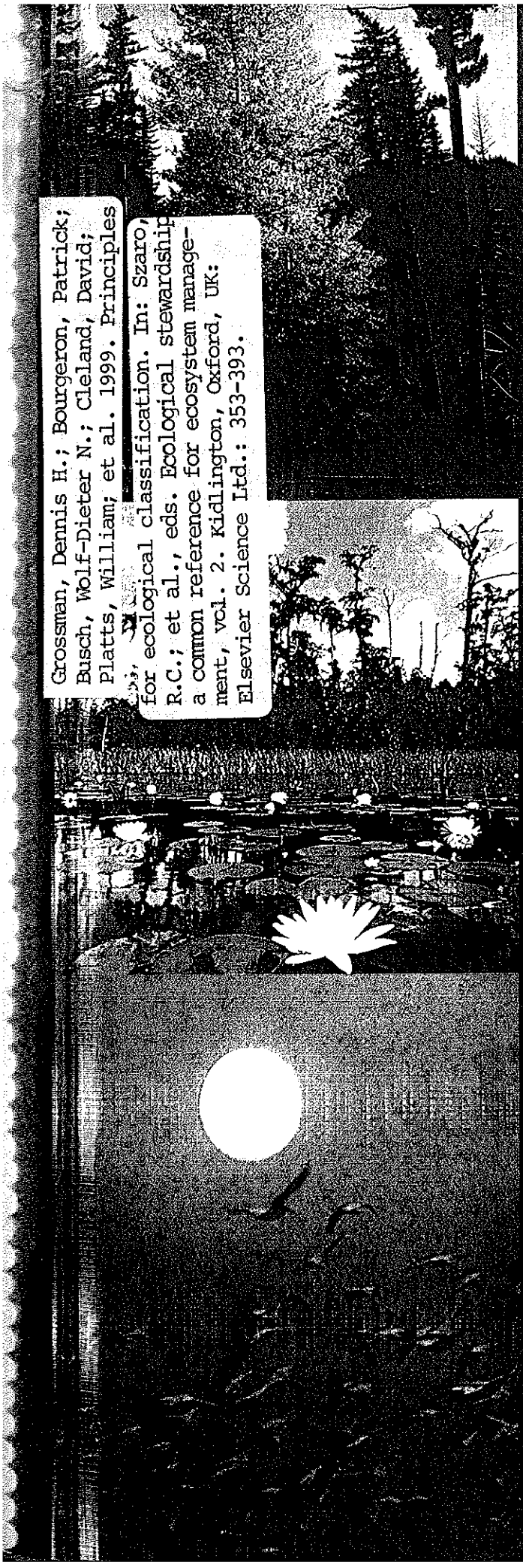

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A practical reference for scientists and resource managers

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Principles for Ecological Classification

Dennis H. Grossman, Patrick Bourgeron, Wolf-Dieter N. Busch, David Cleland, William Platts, G. Carleton Ray, C. Richard Robins, and Gary Roloff

Key questions addressed in this chapter

- *Review of historic and current approaches to ecological classification*
- *Relationship between ecological classifications and management objectives*
- *Strengths and weaknesses in the applications of current ecological classification systems*
- *Role of data and quantitative methods for the development of ecological classifications*
- *Conceptual and practical differences in the development and application of ecological classifications for terrestrial, freshwater and marine ecosystems*
- *Challenges for the future development of integrated ecological classification approaches*

Keywords: Biogeography, ecoregions, vegetation, watersheds, climate, geology

1 INTRODUCTION

The principal purpose of any classification is to relate common properties among different entities to facilitate understanding of evolutionary and adaptive processes. In the context of this volume, it is to facilitate ecosystem stewardship, i.e., to help support ecosystem conservation and management objectives.

This chapter has three purposes. The first is to provide a broad, scientific overview of the theory and methods of ecological classification. The second is to review past and current efforts to shed light on the characteristics of current classifications and how they have evolved. The third is to provide the scientific foundation for applying ecological classification to resource planning and management in the ecosystem context, with a primary emphasis on new paradigms for classification. In all three aspects, the focus is on the United States because the intent is to help meet the goal of improved ecological stewardship of federal lands and waters.

It is now widely accepted that federal management activities should take an ecosystem approach. The goal of this approach to management has been defined by the IEMTF (1995) as follows: "to restore and sustain the health, productivity, and biological diversity of ecosystems and the overall quality of life through a natural resource management approach that is fully integrated with social and economic goals. This is essential to maintain the air we breathe, the water we drink, the food we eat, and to sustain natural resources for future populations."

To this somewhat anthropocentric definition, one may add the importance of maintaining entire landscapes (e.g., Franklin 1993), the conservation of evolutionary and ecological processes, and the protection of species and ecosystems in protected areas (e.g., Grumbine 1994). Virtually all of the approaches have explicit or implicit requirements in common for the application of the best of theoretical science, and for clearly articulated conservation and management goals. Historically, these two requirements have not necessarily been congruent; in fact, they have often been at odds. Yet only through the alignment of ecosystem concepts with realistic management goals may the necessary research and monitoring activities emerge to meet the challenges involved in sustaining productive ecosystems, with their full complement of biological diversity.

Solutions to problems related to the common interests of science and management directly affect ecological classification. In the past, problems were expressed narrowly according to site- or resource-specific goals. This led to narrowly defined classifications specific to those problems. The ecosystem approach is broad and integrative, multi-factorial, and synthetic. Consequently, it is clear that a paradigm shift is required in how classifications may become ecosystem-oriented, dynamic, and process-oriented. Also, they must evolve according to increases in knowledge and to the evolving needs of ecosystem management.

A fundamental question is whether a common classification system can be developed that would meet the needs of all ecosystem managers. The answer seems to lie in the ecosystem concept and the clarification of what is "common" to all ecologically based classifications. For the complex variety of conservation and management questions that will always exist it would appear that a variety of biophysical classifications will always by needed.

This chapter attempts to respond to the challenge of developing common ecosystem properties for ecological classifications. It is structured in five sections. After providing a definition of ecological classification, below, Section 2 describes the theory, conceptual approaches, and methods that have been developed, and that continue to be the basis for, ecological classification. Section 3 is a summary of existing classifications for the major ecological realms — terrestrial, freshwater, and coastal-marine. It will become apparent that each of these realms has been historically treated quite differently, conceptually, and methodologically. In some cases, management applications are made difficult by these contrasting approaches, as for example when aquatic systems are subsumed within terrestrial, floristic provinces.

Section 4 describes how classifications may be derived by means of multi-factor, integrated methods. This approach is required for ecosystems, which are complex, hierarchical, integrated systems involving both biotic and abiotic elements. Section 5 summarizes major existing classification systems and their applications. Section 6 presents conclusions and future needs.

This chapter is written in recognition that no ecosystem classification system yet exists that truly integrates all ecosystem attributes, nor that can suffice for all plants and animals, nor for all lands and waters, nor that can fully describe or predict ecological change. Notwithstanding these limitations, our intent has been to cull out the essential elements of the subject with future needs in mind, trusting that the reader will refer to the literature cited for further insight and information.

1.1 What Is Ecological Classification?

The objective of any classification is to group together sets of observational units based on their common attributes (Kent and Coker 1992). Thus, ecological classi-

fication refers to the development and characterization of a set of units that are assigned by analyzing environmental and biological variables. The variables that can be used for classification are determined by available data and other resources. The end product of a classification is a set of groups derived from the units of observation where units within a group share more attributes with one another than with units in other groups. The ecological stewardship implications are that all representatives of an ecological unit should respond predictably to both natural changes and resource management practices (Driscoll et al. 1984).

Four important historical facts have set the stage for present-day ecological classification. First, classification in the past has been dominated by static approaches; ecological dynamics were poorly understood and environmental change was generally not considered. This is especially apparent on maps, where the polygons do not represent spatial, environmental and temporal dynamics. Second, by far the majority of work on ecological classification has been land-based, resulting in the omission of aquatic features. Third, aquatic systems have been classified generally by means of physical features, such as temperature, salinity, topographic features that define watersheds, the dendritic structures of river systems, estuarine structure, and the like. This is in strong contrast to the more biotic approach of land systems. These segregated treatments of terrestrial and aquatic systems defy attempts at integrating these ecosystem classification approaches, as is obvious in the case of omitting rivers from terrestrial biotic provinces or not considering land-sea interactions when describing coastal classifications. (An assumption for the land has been that vegetation is a surrogate for other biota. An assumption for the sea is that zoogeography or physical features can be used to define oceanographic regions, or vice versa. These assumptions have met with uncertain results.)

Fourth, a host of classifications has resulted from both the fragmented approach of management and the disciplinary approach of science. As a result, some classifications are defined at a single level, whereas others contain multiple levels, which may or may not be hierarchical. Most classification systems, and levels within classification systems, are associated with a particular geographic area and with specific spatial scales for implementation.

It is now abundantly clear that biotic–abiotic, terrestrial–aquatic integration is required for an ecosystem approach to classification. If ecological classification systems are generally to be used to delineate sets of biophysical units across landscapes, they must go beyond climate, floristics, zoogeography or physical features, as sole descriptors for those units. If coastal systems are to be classified, they must be fully based on the interactions of land, sea, and atmosphere, which define the coastal zone.

1.2 Classification Must be Driven by Objective

Different approaches to ecological classification have been developed to address specific objectives. As reviewed in this chapter, numerous ecological classification systems have been applied in many different areas over the years. There is no one correct way to classify ecosystems; the success of an approach is measured by its ability to meet management and/or scientific objectives, preferably both when they exist. Classifications have primarily been constructed for three purposes: (1) to help develop and represent the science of biogeography itself; (2) to help identify "representative" ecosystems for protection, restoration production, management, research, monitoring, and inventory, most notably of living resources; and (3) conservation of biological diversity. With respect to management itself, many possible applications exist for classifications, of which Frayer et al. (1978) have identified four: (1) a basis for cataloging the status of current resources; (2) a means of transferring experience and knowledge of a studied area to a similar but unstudied area; (3) a framework for assessing local management opportunities and predicting the outcomes of treatments or actions; and (4) a vocabulary for communication between managers, between managers and researchers, and between managers and the public.

The principal factor that controls the relationship between classification and objectives is scale. For example, ecological classification requirements for songbirds (functioning at the vegetation stand level) are different than those for amphibians (functioning at the micro-habitat level). However, under a properly designed system, ecological units that are appropriate for management objectives related to amphibians can be aggregated into or nested within units meaningful for songbird management. Thus, the first step in ecological classification is to determine the spatial scales needed to address management objectives.

Historically, management objectives have emphasized single resources as separate entities in the landscape or seascape. Contemporary land managers, however, are asking new sets of questions that require integration of multiple factors. These new questions include:

- What are the cumulative effects of a management activity on multiple components of a system?

- Will a management activity disrupt the inherent ecological processes and functions of the system?
- What level of a management activity will direct the system into an aberrant ecological trajectory?

Such questions are the essence of ecosystem stewardship because they place resource management in the context of multifaceted, hierarchical, ecological relationships. This is a particular challenge for the integration of science and management, as science is not able to give answers with high degrees of certainty to such questions. An instructive example concerns fisheries management, which has been treated from the point of view of simple "yield" models, out of context of ecosystem properties. A growing concern is that of sustained ecosystem functions and processes over time in light of management actions (question 3). Orians (1975) defines the following measures of ecosystem "stability": (1) constancy, (2) persistence, (3) inertia, (4) elasticity, (5) amplitude, (6) cyclical stability, and (7) trajectory stability. Which measures are operational can be very difficult to identify, but these terms define a way to approach ecological classification from a functional-process viewpoint.

2 HISTORICAL OVERVIEW OF ECOLOGICAL CLASSIFICATION

Biogeographic classification has a very long history, with strong links to biological diversity and biogeography. Since the time of the Greek scholars Aristotle and Theophrastus during the third century B.C., and of the Latin scholar Pliny the Elder during the first century A.D., descriptions of species have been accompanied by classifications, however rudimentary, and data on site locations. Over subsequent centuries to the present, many questions concerning the characterization of biological species and communities, including their relationships to environmental and latitudinal gradients, have emerged. As a result of rapid discoveries and the increasingly disciplinary nature of the inquiry, many different approaches to biological and ecological classification have been developed, along with a massive literature.

Historical approaches to ecological classifications may be broadly characterized as being either locally specific or regionally simplified. For local classifications, there has generally been a highly focused objective and a large quantity of field information; this has resulted in classifications and maps that are specific and detailed. In contrast, regional treatments have tended to generalize data from few points over large areas and, thus, had limited use at a local level. The most important contemporary advances have utilized the greater availability of biotic and abiotic data and improved spatial technologies to create multiple hierarchical classifications that can be applied to different objectives at multiple scales. What may be described as "local" vs. "regional" differs markedly among various systems. For the land, the difference is apparent. But for rivers, the watershed is the usual "regional" frame of reference, with "local" referring to third- or fourth-order tributaries. For coastal systems, "regional" is the biotic province, usually defined by the ranges of endemic fauna; "local" refers to physical subunits such as estuaries, bays, tributaries, and coastal formations. For open marine waters, including both coastal oceans and ocean basins, "regional" may refer to zoogeographic provinces or water masses; "local" is usually referred to as "sample sites" or "patchiness."

Ecological classifications have historically been based on abiotic, biotic, or integrated approaches. Abiotic classifications have defined sites and mapping units by singular or multiple components of the abiotic environment. These components include land forms (Hammond 1964), physiographic provinces (Fenneman 1928), and climate (Trewartha 1968), along with other variables such as geology, watersheds, and elevation. Biotic classifications have primarily been developed to portray vegetation classes and animal habitats.

Examples of terrestrial biotic classifications include potential natural vegetation (Küchler 1964), vegetation physiognomy (UNESCO 1973, Grossman et al. 1994b), Society of American Foresters cover types (Eyre 1980), plant communities (Grossman et al. 1994b), and natural vegetation of the Southwest (Brown et al. 1980). Hybrid approaches have integrated abiotic and biotic components to classify and map actual or potential land units. Examples of integrated approaches include habitat types (Krajina 1965, Pfister et al. 1977), ecoregions (Bailey 1976, Omernik 1987), forest regions (Braun 1950, Rowe 1972), ecological land units (Haufler 1994), and wetlands (Cowardin et al. 1979).

In Europe, land use planning assessments prompted the development of ecological classification in the early 1930s. Ecological, as opposed to purely biotic, classifications attempt to interpret the ecological meaning of the distribution of biotic types by relating this distribution to one or more features of the environment. Tools such as "ecological vegetation maps," which noted the environmental features believed to be indicated by the vegetation, were used for large-scale assessments of the suitability of sites for particular uses (Zonneveld 1988). Similarly, the North American concept of "ecosystem" became the basis for evaluating suitability in that site characteristics for a given

mapping unit were used to determine appropriate land use categories and for other resource management needs. In the United States from 1900 to the late 1960s, resource management was mainly concerned with protection from catastrophic events (e.g., fire, floods), and with the efficient extraction of commodities. Throughout the 1970s and 1980s, however, an increased environmental awareness on the part of the public and within government confirmed and strengthened the need for structured, ecological data assessment tools. Single-factor classification systems were ineffective at addressing these "new" issues and did not capture land functions and processes. As a result, multi-factor ecological classification systems that recognized system inputs, outputs, complexity, and inter-connectedness were developed to address multiple-use and biodiversity issues.

Terrestrial classification systems have historically been given more attention and are considerably more advanced than other classification systems. As a result, aquatic systems tend to be included within terrestrial systems. For example, Bailey (1995) described "ecoregions" on the basis of land surface, climate, vegetation, soils, and fauna. This approach neglects watersheds and their dynamics and even the existence of the coastal zone, which includes a major portion of the land surface. Additionally, Cowardin et al. (1979) described wetland and deepwater habitats in traditional, typological ways that did not take into account the dynamic approaches employed by coastal biologists and oceanographers.

Coastal-marine physiographic and biogeographic classification has its own long history, perhaps dating from the scientific voyages of the 19th century. Modern zoogeography was initiated by Ekman (1953) and Hedgpeth (1957), who took zoogeographic and physical-ecological approaches to sub-dividing the near-shore seas and oceans into now-familiar zones (from littoral to abyssal). Somewhat later, Briggs (1974) re-evaluated the zoogeography and proposed a system of coastal biogeographic provinces primarily based on endemic species. This method allows clear identification of province divisions, but does not create a relational basis among provinces for evaluation, as all provinces defined by endemism become, by definition, unique. Nonetheless, Briggs's approach does confirm divisions that have long been apparent among coastal biotic provinces (e.g., as given for North America in Robins and Ray 1986, Robins 1992).

A major, relatively recent development has been the recognition of the "coastal zone" as a distinct earth realm where land, sea, and atmosphere uniquely interact. Ketchum (1972) essentially defined this zone to include the entirety of the coastal plains and continental shelves of the world. This zone is now estimated to include sea level plus and minus 200 m. It encompasses 18 percent of the earth's land surface and 8 percent of the oceans' surface (but less than 0.5 percent of the oceans' volume). However, its importance is disproportionate to its size: it supports 60 percent of the human population, and accounts for a quarter of the global primary productivity and more than 90 percent of fisheries (LOICZ 1996). The recognition of the coastal zone warrants a new ecological classification that not only transgresses traditional land–sea boundaries, but also functionally integrates terrestrial, marine, and atmospheric processes.

The need for a global classification of coastal and marine systems became especially clear when IUCN and UNESCO recognized during the 1970s that there was no comprehensive, global classification for conservation purposes. Udvardy's (1975) "world" classification was intended to meet that need for the land, but this "world" did not include freshwater and marine systems. Consequently, IUCN and UNESCO supported an effort to develop a matching, coastal-marine classification. The result was Hayden et al. (1984), which reviewed the "state-of-the-art" and presented a tripartite scheme for comparing coastal geomorphological provinces, coastal biotic provinces, and marine realms. It was recognized that this scheme needed significant extensions, particularly into the third dimension of deeper ocean waters and into smaller scales of interaction. However, to date, this global treatment has not been expanded.

In summary, most work on ecological classification and the related field of biogeography has focused on specific systems or elements of systems. There are many examples of classifications that represent specific taxa, landforms, vegetation and climate, physical geography, the phytoplankton of oceanic waters, estuaries and habitats of continental shelves, coral reefs, and other factors. It has become increasingly clear that many of the challenges presented by management of whole ecosystems cannot be addressed by these fragmented classification approaches.

3 ECOLOGICAL CLASSIFICATION: THEORY AND METHODS

From this brief history, it is clear that ecosystem management requires a reversal of trends, in both science and management, away from fragmentation and reductionism. The Ecological Society of America (ESA) has led attempts to define concepts for holistic management application, e.g., for "sustainability" (Lubchenco et al. 1991). More recently, the ESA has reported on the scientific basis for ecosystem management,

defined by: "...explicit goals, executed by policies, protocols, and practices, and made adaptable by monitoring and research based on our best understanding of the ecological interactions and processes necessary top sustain ecosystem composition, structure, and function" (Christensen et al.1996). This amplifies the definition of the IETMF (1995) to include specific scientific goals, as well as social ones. Among the elements included in ecosystem management, as defined by this ESA report, are: sustainability, ecological modeling, adaptability and accountability, spatial and temporal scale, ecosystem function and dynamics, ecosystem integrity, and the uncertainties of our knowledge.

3.1 Theoretical Basis for Ecological Classification

In this context, it is abundantly clear that most present classifications are incomplete and possibly even misleading in cases where the approaches are based on narrowly defined ecosystem components. To address future ecosystem-oriented needs, seven areas of ecological theory need to be considered: (1) pattern recognition; (2) system dynamics; (3) hierarchy theory; (4) systems limits; (5) the biotic component of ecosystems; (6) the abiotic component of ecosystems; and (7) ecosystem characterization. Each of these areas is described in greater detail below. The treatment of these issues affects the selection of the concepts guiding ecological classifications, the most appropriate data for such classification, the best techniques for classifying ecosystems and their components (e.g., assemblages of species, landscapes, seascapes), and the best methods for predicting ecosystem properties and their responses to various management scenarios.

3.1.1 Pattern Recognition

To describe ecological systems, pattern recognition techniques are often employed. But because ecosystems are complex systems, defined by exchanges of energy, materials, and information, which may be described at many different scales (Levin 1992), their boundaries may be difficult to define and may even be considered arbitrary. Nevertheless, boundaries are determinable, for example, by recognizing gradients or "ecotones," which also provide a context for understanding ecological function (Hansen and di Castri 1992).

Ecological classification requires that spatial and temporal relationships need to be defined clearly (Bourgeron and Jensen 1993, Jensen et al. 1996). Furthermore, ecosystem management requires making predictions about ecological systems, that is, determining relationships between patterns and hypothesized causal factors (Urban et al. 1987, Bourgeron and Jensen 1993, Jensen et al. 1996). Once a correlation or a cause–effect relation between pattern and process is determined, predictions are made using the summary of data and information performed during the classification process and/or the generation of maps, statistical or simulation ecological models, and/or a combination of the first two approaches. Such interpretations are reasonably well developed for terrestrial systems, but are only at a primitive stage of development for coastal (Ray 1991) and marine (Steele 1989, Ogden et al. 1994) systems.

3.1.2 System Dynamics

Most existing ecological classifications are concerned with patterns or static structures. However, ecosystems may exhibit several trajectories (Orians 1975), and future ecosystem classifications cannot ignore these dynamics. A new approach is that of dynamic biogeography, which merges the large-scale approaches of traditional biogeography with smaller scale approaches of ecology. Dynamic biogeography concerns the study of biological patterns and processes on broad geographical and time scales, and represents spatial patterns at different scales of variation (Hengeveld 1990).

Ecological classifications are used for many purposes, such as assessing spatial relations and comparative features of ecological systems. However, ecological systems exhibit temporal changes along various developmental pathways that result in different types of organization. Many conceptual models used for planning purposes assume that all ecosystems reach a state of equilibrium or quasi-equilibrium (e.g., the assumption that succession leads to climax). However, we now know that ecosystems are rarely in equilibrium. Although it is convenient for scientific (e.g., modeling) and planning purposes to assume equilibrium at a given scale, we must recognize that ecological systems are fully dynamic (e.g., Kay 1991, Constanza et al. 1993). Thus, ecological classifications at all scales need to be designed to account for change, which may be slow or rapid, in terrestrial and aquatic systems.

3.1.3 Hierarchical Organization

Complex ecosystem patterns, and the multitude of processes that form them, exist within a hierarchical framework (Allen and Starr 1982, Allen et al. 1984, O'Neill et al. 1986), as is readily observed in landscapes or seascapes. In recent years, considerable attention has been directed to describing this hierarchical organization. Hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986) views multi-scaled systems as a

series of constraints in which higher levels of organization provide the environment in which the lower levels function. However, constraints are not necessarily "top-down," as Holling et al. (1993) have described. Ecosystems at any level may cycle through functional states of "exploitation," "conservation," "release," and "reorganization," in which both "top-down" and "bottom-up" interactions are evident.

Four tenets of hierarchy theory are critical to understanding landscape patterns and their dynamics, and to using that knowledge for ecosystem management (Allen et al. 1984; O'Neill et al. 1986).

1. Every component of a system, ecological or otherwise, is both a whole and a part at the same time. This concept is called "whole/part duality." For example, a forest (a whole) is made up of trees (the parts), each of which would consist of multiple communities for many organisms. At a larger spatial scales, the forest is part of a larger scale regional landscape.
2. Patterns, processes and their interactions can be defined at multiple spatial and temporal scales. These scales need to be identified clearly, according to the question being asked or the function being examined.
3. There is no single scale of ecological organization that can be used for all purposes. This is important to consider because ecological systems are often interpreted at a single scale or at a limited number of scales.
4. The definition of the component patterns and processes of any particular ecological hierarchy is dictated by the objectives of the study or by the objectives of management.

Most classifications are static and "taxonomic," whereas hierarchy theory challenges them to become dynamic and integrative. The "whole/part duality" of ecosystems (Koestler 1967, Allen and Starr 1982, Allen et al. 1984) clarifies ecological classifications because hierarchy theory expresses how different levels of ecological organization are linked. The findings at any one level may assist the understanding of another level, but can never fully explain phenomena occurring at other levels (Odum 1971). That is, each level of a hierarchy has characteristics that can only be explained with knowledge of other levels.

3.1.4 System Limits

As noted above, ecological systems may follow different trajectories of change. Much attention has been given to whether natural change is limited to approaches to a "climax" state in which an ecosystem functions at an "optimum." For example, it has been assumed that, eventually, ecological succession continues until species stop replacing each other, at which point the processes that lead to change balance the processes that lead to ecological organization. At this stage, called "climax," the ecosystem presumably would be operating at "optimum." Yet actual field observations reveal that this point does not remain constant. Environmental conditions may change (e.g., because of local, regional, or global climate change), new species may appear, and, even in the absence of major disturbances such as regional fires or coastal storms, the "climax" will change to a new community. The result is an "altered ecosystem state" with different optimal conditions (Hayden et al. 1991).

Obviously, the concept that optimal limits exist for any ecological system deserves re-examination. The observed state of an ecosystem may be only one of several possible and, hence, that the concept of an "optimum operating point" at "climax" may be misleading. It has been assumed that if an ecological system follows one path rather than another in response to disturbance or environmental change, it may operate far below its optimal level. An example is the maintenance of prairie grasslands under the natural disturbance regime of low intensity, high frequency fires. When such fires are suppressed, succession leads to the development of a forest stage (e.g., Arno and Gruell 1985). Thus, the conclusion was that the ecosystem functioned at suboptimal levels under presettlement disturbance regimes. On the other hand, disturbance is known to increase the biological diversity of some systems, notably tropical rain forests and coral reefs (Connell 1978), and recent research has shown that an increase in biological diversity may increase the productivity of ecosystems (Naeem et al. 1994).

Ecological classifications need to be designed to reflect these factors, especially if they are to be used in ecosystem management or assessments. This is especially important because many of the ecological units that require protection and management do not represent late successional or "climax" stages and/or are not in a state of equilibrium.

3.1.5 Biotic Component

Species patterns over time and space may be used to define the biotic component of ecosystems in two ways: by means of the continuum or community concepts. The continuum concept states that species assemblages are temporary and fluctuating phenomena along regional gradients. In contrast, the community concept maintains that repeatable assemblages of species occur in discrete habitats with characteristic

properties. The conflict between these two approaches has far-reaching implications for ecological classification. For example, if the continuum concept is correct, the biotic component of ecosystems cannot be classified because species respond individualistically to environmental change over space and time. Most researchers implicitly accept the continuum concept, even avoiding the term community and referring to the more neutral term "assemblage" (Austin 1991). The same researchers, cartographers, and other practitioners, however, continue to recognize homogeneous units, hence implicitly using the community concept for pragmatic management purposes.

In defining the biotic component of ecosystems, finding a practical approach has faced major limitations. Weak and ambiguous classifications have resulted from unspecified or inconsistent criteria, vague definitions of key concepts, unspecified minimal areas of reference, and undocumented sorting strategies (Whittaker 1978, Küchler and Zonneveld 1988). In addition, existing data have not supported rigorous testing among the various continuum alternatives (Austin 1991). Nevertheless, various aspects of both the continuum and the community views appear to complement rather than exclude each other (Westhoff and van der Maarel 1978, Whittaker 1980, Austin 1991). It has been shown, at least for terrestrial vegetation, that species can be individually distributed along gradients (Austin 1987, Austin and Smith 1989) *and* that the distribution pattern of controlling environmental factors constrains the pattern of species combinations, their distribution in the landscape, and their frequency.

Even if some form of the community concept is accepted, the problem of identifying the full set of environmental factors shaping the composition of the biotic community remains. For terrestrial classification, the concept of a floristic or biotic province is defined within the context of a region with a distinct pattern of climate and landscape characteristics (Bailey et al. 1994). This is because such classifications are useful for defining regional ecosystem management guidelines only if vegetation units, defined as biotic or floristic provinces, or any variant (e.g., Küchler 1967, Brown et al. 1979) are modified to correlate with climatic/landscape regions (Burger 1976, Rowe 1980, Bailey and Hogg 1986, Küchler 1988). A primary purpose of such regionally defined ecosystems is to serve as a reporting structure for information about regional resources and environment (Bailey and Hogg 1986, Bailey et al. 1993). Another purpose is to define homogeneous regions within which to characterize finer scale ecosystems and/or landscape properties (Westhoff and van Der Maarel 1978, Austin and Smith 1989). Similarly, attempts to characterize landscape level ecosystems and conduct landscape assessment using such communities can be successful only if the intra-community pattern of gradual change is correlated with gradual changes in the environment. Therefore, effective landscape surveys need to take into account this dependence of biotic patterns on abiotic variables (Bourgeron et al. 1993).

The extent to which regional climatic/floristic classifications may apply to the fauna or to aquatic systems is highly dependent upon the strengths of the ecological linkages or dependencies among these different components. It would be incorrect to assume, for example, that different taxa respond in the same way to a particular set of environmental variables. Bibby et al. (1992) reported that areas of high endemism for birds are not the same as those for other vertebrates. Freshwater fishes are distributed according to the confines of watersheds, not floristics, and aquatic-coastal biotic provinces (Hayden et al. 1984) appear only roughly related to adjacent terrestrial provinces (Bailey 1995).

3.1.6 Abiotic Component

Two major categories of abiotic environmental variables have been useful for ecological classification (Austin et al. 1984, Austin 1985, Austin and Smith 1989):

- indirect factors — known to be correlated to direct factors that exert physiological influence on species (e.g., elevation, bathymetry);
- direct factors — known to have a direct physiological influence on species (e.g., temperature, pH, nutrients). Both of these have been variously been used for classification of terrestrial, freshwater, and marine systems.

Numerous assumptions are made in developing ecological classifications that involve the abiotic components of ecosystems. The first maintains that biological communities are surrogates for the environment. This approach, for example, uses the vegetation as a surrogate for the environment as a whole, based on the assumption that vegetation is a faithful expression of site characteristics (Troll 1941, 1943, 1955, 1956; Küchler 1988). Therefore, vegetation maps have been central to describing ecological patterns (Whittaker 1980). Similarly, for deep oceanic systems, plankton diversity has been used for decades as an indicator of environmental conditions for the delineation of ocean zones (McGowan 1971, Dunbar 1979).

The second assumption is that ecological units contain recurrent patterns and characteristics that can be delineated. This approach uses broad environmental patterns alone to describe and delineate abiotic elements in both terrestrial (Rowe and Sheard 1981,

Zonneveld 1989) and coastal systems (Hayden and Dolan 1976).

The third assumption is that environmental patterns may be integrated with biotic patterns to describe and delineate habitats of both plant and animal communities. For terrestrial systems, classifications have been developed using climatic attributes either alone or in conjunction with other attributes (e.g., Bailey 1976, Austin and Yapp 1978, Walter 1985, Omernik 1987, Bailey et al. 1994). For aquatic systems, very different approaches are used for freshwater, estuarine, and marine systems (Section 3.2).

A fourth assumption is based on the argument that, to be meaningful, ecological evaluation should be based on species' niche–habitat relationships (e.g., Hutchinson 1959, Whittaker 1972, Nix 1982, Brown 1984). The aim is to summarize environmental variability, identify the distribution of major environmental gradients, and indicate where significant shifts in ecological variability might occur (Mackey et al. 1988, 1989). To accomplish this, species' responses to a limited set of dominant environmental variables that comprise primary niche dimensions must be estimated (Nix 1982; Mackey et al. 1988, 1989). Site-specific data are used to generate classes of sites sharing similar ranges of values of the environmental variables. A map of these classes, or bioenvironments, can be used alone in the ecological assessment stage of an area for given purposes (DeVelice et al. 1993), and/or in conjunction with vegetation data for quantifying biotic–abiotic correlations (Mackey et al. 1989).

In all cases, the classification units arguably represent natural levels of ecosystem integration with respect to environmental regimes and key processes - and there is evidence that this is the case (Swanson et al. 1988). For example, geomorphic pattern, through erosional/sedimentation processes, controls carbon, nitrogen, and phosphorus cycles in soils of riparian forests in southern France (Pinay et al. 1992).

3.1.7 Ecosystem Characterization

In the field, various ecological classifications are often used together to delineate the boundaries of ecological systems. For example, a classification of the vegetation may be used with classifications of land forms and disturbances. The process of using ecological classifications for matching patterns and processes is called ecosystem characterization (Levin 1992). This process is used for mapping (e.g., Avers et al. 1994, Zonneveld 1989) and landscape evaluation from the site to the continent level. In defining ecological land types (e.g., Wertz and Arnold 1972), the idea is to draw boundaries around ecological systems. Relevant patterns and agents of pattern formation at all appropriate ecological and planning scales may then be defined. The proper match of patterns and agents of pattern formation is important because any incorrect coupling of pattern to agents impedes the ability to make predictions about the future state of the ecological system. As a result, the value of conservation and management actions and prescriptions is limited.

3.2 Goals and Methods of Multivariate Classification

The introduction to this chapter defined the purpose of ecological classification in the context of meeting the goal of ecosystem management. Sections 2.1 and 2.2 described past approaches and presented some aspects of modern ecosystem theory as a setting for future development. Clearly, classifications are now challenged to become integrative, dynamic, and adaptive. Accordingly, this section reviews some multi-factor methods and their applications.

Developing ecological classification systems is an iterative process involving field observation, statistics, and numerical modeling. At fine spatial scales, ecological units are often identified in the field, based on such things as flora, soils, and physiography (Host et al. 1988). At coarser scales, data from remote sensing or other sources are commonly analyzed (Denton and Barnes 1988). Classification units are refined as additional sampling and analyses are completed, and new relationships among components are identified. Additionally, sampling of ecosystem components aids in the recognition of such patterns as soil–vegetation correlations. This information is then integrated into the classified units.

Once large data sets are on hand, a variety of multivariate methods may be employed to identify patterns and to reduce the number of variables. Multivariate methods have been used to detect patterns in different types of data, including overstory basal areas, ordinal ground flora coverages, and nominal soil texture classes (Cleland et al. 1993). Also, statistical methods can be employed to simplify data sets by extracting their "principal components," as has been done for estuaries by Ray et al. (1997) through the analysis of NOAA's (1985) large data set. Several methods have been widely applied in recent years to the analysis of flora, fauna, plankton, abiotic features, and whole environments (e.g., estuaries), especially where it is necessary to condense and summarize extremely large data matrices.

Multivariate ecological classifications for terrestrial and aquatic environments have changed dramatically over the past few decades. Historically, analysis was

carried out through the tabular analysis of plot data. Braun-Blanquet's procedure of 1921 used tabular methods in successive approximations to identify groups of species occurring in similar samples, and to identify samples with similar species composition. These early tabular classification techniques were informal and inherently subjective (Whittaker 1962, Mueller-Dombois and Ellenberg 1974). As a result, recognizing different species groups as well as groups of similar samples depended heavily on the individual investigator's understanding of species-species and species–environmental relationships within a study area. The results have been variously expressed in tables, dendrograms, and maps.

The past few decades have seen the proliferation on more objective procedures and refined multivariate analyses, in some cases leading to models expressive of ecosystem function (Mueller-Dombois and Ellenberg 1974, Gauch 1982, Spies and Barnes 1985, Denton and Barnes 1988, Hix 1988, Host and Pregitzer 1991, Bulger et al. 1993). These procedures include explorative data analyses involving descriptive statistics and graphical displays that are used to: (1) detect intercorrelations among variables, thus reducing in the number of variables that need to be considered; (2) check assumptions about the data structure underlying particular analyses; (3) suggest appropriate transformations; and (4) identify sample outliers.

3.2.1 Ordination

Ordination is a powerful technique used to identify important variables, to summarize data, and to reduce the complexity of the data set. The results may be displayed diagrammatically or mapped. In ecological studies, ordination is also used to discover the latent structure of data by analyzing species' responses to underlying environmental gradients (Prentice 1977, Bulger et al. 1993).

Principal component analysis (Gauch 1982, Morrison 1976), correspondence analysis (Hill 1974, Greenacre 1984), and detrended correspondence analysis are among the most commonly used ordination techniques in modern ecological studies. They employ different methods to account for the variance in the data.

Ordination is often used in an exploratory sense to detect trends as well as outliers, to screen variables, to reduce dimensionality, and to summarize community and environmental patterns. Ordination is often accompanied by clustering procedures to clarify natural groupings of sampled data. Results of ordination and clustering may be compared, and subsets of data may be interrogated to elucidate relationships further and to develop hypotheses. Several complementary analysis techniques may be applied to the same data set. The communication of results is promoted by employing a moderate number of commonly used, relatively standardized methods (Pielou 1977).

3.2.2 Clustering

The objective of clustering is to identify naturally occurring groups based on all variables in a data set. Both the process and the choice among techniques are more complex and more subjective than those of ordination. The most commonly used clustering methods are: (1) non-hierarchical, (2) polythetic hierarchical agglomerative, and (3) polythetic hierarchical divisive. Non-hierarchical clustering assigns data to clusters, placing similar samples or species together. This is an excellent way to handle redundancy and outliers, but is limited in its ability to analyze relationships. Hierarchical clustering also groups similar entities together into classes, but additionally arranges these within a hierarchy such that a single analysis may be viewed on several levels, with relationships expressed among the entities classified. The utility of a given technique is judged in relation to others, and often several classification techniques are applied to the same data sets with results compared afterwards.

The term "polythetic" means that information on all variables is used to assign observations to a cluster, as opposed to earlier monothetic methods that used single variables in a non-multivariate analyses. Polythetic agglomerative clustering has two steps: (1) the samples-by-species data matrix is used to compute a samples-by-species dissimilarity matrix using any of several distance measures such as Euclidean distance or percent dissimilarity; (2) an agglomeration procedure is applied successively to build up a hierarchy of increasingly large clusters, starting with clusters consisting of a single member, and agglomerating these hierarchically until a single cluster contains all the samples or species. The polythetic hierarchical divisive method similarly computes the dissimilarity matrix in the first step, and then successively applies a divisive procedure to a single large cluster to create a hierarchy of individual members.

The simplest polythetic-divisive classification is ordination space partitioning (e.g., Noy-Meir 1973, Peet 1980). Two-way indicator species analysis (TWINSPAN) (Hill 1979) is another polythetic divisive clustering technique. TWINSPAN begins with all species or samples (depending on the objectives) in a single cluster and divides these into smaller clusters by first ordinating data by reciprocal averaging. The reciprocal averaging procedure is repeated until each cluster has no more than a chosen minimum number of members.

3.2.3 Summary

Presently, ecological classification is often approached in an combined program of ordination, clustering, direct gradient analysis, and tabular synthesis of results. A five-step procedure has become routine, especially for terrestrial systems where procedures are most advanced. The analysis progresses by successive stages of refinement (Cleland 1996). First, exploratory data analyses are conducted to ensure that the assumptions underlying particular methods are met, and to reduce the number of variables. Second, ordination is used to summarize community and environmental patterns. Third, clustering is used to identify groupings of samples and variables, and to corroborate patterns detected through ordination. Fourth, community patterns are compared with environmental information to elucidate congruent changes and to produce an integrated interpretation of the ordination and clustering results. Finally, hypothesis testing methods may be used *a posteriori* to assess the relationship between classification and mapping as well as the ecosystem-level differences in structure and function. Such differences might include biomass production and productivity (Host et al. 1988), successional pathways (Host et al. 1987, Johnson 1992), and nitrogen dynamics (Zak et al. 1986, 1989).

Thus, multivariate methods are extremely useful in ecological classification because of the large number of variables and observations commonly analyzed, the difficulty in detecting patterns due to the complex interrelationships involved, and the need to verify the taxonomic and spatial hypotheses represented by classification and mapping. Multivariate analyses alone, however, are insufficient to develop classification systems. Even though the analysis methods themselves may be relatively objective, the selection of particular multivariate methods, decisions about how to standardize data, the selection of important variables or the removal of superfluous, redundant, or rare variables are subjective choices that can influence the resulting classification. In addition, the experience gained through reconnaissance, observation, and field sampling, and through the thought processes required to develop an integrated ecosystem classification, is valuable and *should be* used to augment strictly mechanical methods. The role of multivariate analysis, therefore, is that of a tool to be used in conjunction with knowledge of ecological relationships gained in the field.

4 ECOLOGICAL CLASSIFICATION SYSTEMS

Various types of classifications are summarized in this section, to illustrate their objectives and priorities. All classifications have the goal of determining the relative degree of similarity and difference among units. However, it is apparent that none comprehensively addresses the holistic character of ecosystems. This is not to say that they are not useful, but that integrated, ecological classification still lies ahead. It is also apparent that a classification is most useful to management when it can be mapped and related to biogeography (e.g., Pielou 1979, Brown and Gibson 1983).

4.1 Terrestrial Classifications

Most terrestrial classifications are biotic in nature, although many incorporate references to physiognomic regions and climatic zones. Terrestrial classifications are often simpler than aquatic classifications because of the comparably static nature of landforms and vegetation. Also, more research has been completed in terrestrial systems than in aquatic systems. As a result, terrestrial classifications are more advanced in theory and in practice than are aquatic classifications.

4.1.1 Vegetation Classification

Most terrestrial, biotic classifications have been based on vegetation. Beginning with the viewpoint of Gleason (1917, 1926) and extended by others (e.g., Whittaker 1956, 1962; Curtis 1959), it was generally believed that vegetation units could not be defined. The approaches taken often became polarized between the "continuum" and the "community unit" concepts, described above. But despite differing viewpoints, several features became widely recognized (Mueller-Dombois and Ellenberg 1974): (1) similar species combinations recur; (2) no two sampling units are exactly alike; and (3) species assemblages change more or less continuously if a geographically widespread community is sampled throughout its range. Thus, recurring species combinations may be correlated with their environments, and these combinations shift geographically, meaning that a limited degree of ordering *is* possible.

Potential Versus Existing Vegetation

Two differing approaches to the classification of vegetation are the portrayal of existing versus potential natural vegetation (PNV). Classifications emphasizing existing vegetation determine vegetation units from the current characteristics of the vegetation. Classifications emphasizing potential natural vegetation use characteristics that represent the most mature conditions of vegetation development (Tüxen 1956, Küchler 1964). It is, however, difficult to model the

relationships between existing vegetation and potential natural vegetation. This modeling is limited by the current knowledge of vegetation-site relationships, and the ability of the observer to infer these relationships (Cook 1995). These models also emphasize hypothesized climax vegetation, a concept that is fraught with theoretical and practical difficulties. For example, most existing schemes assume that exotic species will be replaced by native species when, in fact, the behavior of exotics is notoriously complicated to predict.

Basic Classification Approaches

Three vegetation classification systems have gained widespread acceptance: physiognomic classifications, floristic classifications, and combined physiognomic–floristic classifications (Howard and Mitchell 1985). All three approaches provide a systematic ordering of vegetation or ecosystem pattern and relate these patterns to ecological processes. Beginning in the 19th century with the work of plant geographers such as Humboldt, Warming, and Grisebach, vegetation classification focused on the physiognomy of the vegetation. Broadly speaking, physiognomy refers to the structure (height and spacing) of the vegetation and to the life forms of the dominant species (i.e., gross morphology and growth aspect of the plants). In addition, physiognomy refers to characters of seasonality, leaf shape, phenology, duration. These features are relatively easy to recognize in the field with limited knowledge of the flora. Physiognomy provides a fast, efficient way to categorize vegetation and can often be linked to remote sensing signatures. These characters are also useful for initial reconnaissance of areas to be surveyed. In addition, they permit generalizations about the vegetation at a coarse, often worldwide, scale.

The principles underlying physiognomic classification are that each specific life form represents a strategy (Stearns 1976), and that the composition of life forms in a vegetation type is governed by these strategies (Raunkier 1937, Monsi 1960, Walter 1973, Whittaker 1975). The predominance of certain physiognomic types in a region tends to correspond to major climatic zones. Thus, physiognomic categories are often expressions of macroclimate, soils, and vegetation (Holdridge 1947, Walter 1985, Howard and Mitchell 1985).

The basic unit of physiognomic classifications is the "formation," i.e., a "community type defined by dominance of a given growth form in the uppermost stratum ... of the community, or by a combination of dominant growth forms" (Whittaker 1962). These classifications emphasize a "top-down," divisive approach, which in practice, defines formations defined by varied, conventionally accepted combinations of growth-form dominance and characteristics of the environment.

Floristic methods characterize the species themselves. Early 20th century ecologists who favored a strict floristic system included members of what has been termed the Zurich–Montpellier Tradition in central Europe (Shimwell 1971). The most well known among them is that of Braun-Blanquet (1928), who called plant associations with common diagnostic species "alliances." Nowadays, the most commonly defined floristic unit is known as the "association," defined by Flahault and Schroter (1910) as "a plant community ... presenting a uniform composition and physiognomy, and growing in uniform habitat conditions." This definition implies that associations sharing a certain physiognomy would be grouped together into the same formation. Some floristic methods focus on species that occur constantly throughout a set of stands; others emphasize indicator or diagnostic species, which are dominant in or restricted to these stands. Floristic methods require intensive field sampling, detailed knowledge of the flora, and careful tabular analysis of stand data to determine diagnostic species groups. These methods reflect local and regional patterns of vegetation and are more detailed than physiognomic methods. They also provide detailed descriptions of biotic communities regardless of their successional stage or origin. As such, they are typified by an agglomerative, "bottom-up" approach. Thus, floristic units have been used frequently as indicators of ecosystem processes and are a useful component of ecosystem classifications (Mueller-Dombois and Ellenberg 1974, Rowe 1984, Strong et al. 1990).

Combinations of these two approaches have also been developed on the basis that vegetation is most thoroughly described by both structure and floristic composition. As stated previously, physiognomic systems are easily recognized in the field, can be applied with limited knowledge of the flora, permit generalizations of vegetation patterns over large areas, and can be linked to remotely sensed data to facilitate vegetation mapping. In contrast, floristic information is almost always used for detailed site analyses, whether for studying environmental gradients, ecological site factors, or describing and forming classification units. Furthermore, studies have shown that a very good fit exists between floristic and physiognomic classifications because both types of attributes are borne by individual species (e.g., Rübel 1930, Westhoff and Held 1969, Webb et al. 1970, Wergner and Sprangers 1982, Borhidi 1991). The Nature Conservancy (Grossman et al. 1994b; Grossman et al. 1998) have refined the

CLASSIFICATION HIERARCHY

SYSTEM — Terrestrial

PHYSIOGNOMIC CLASS — Woodland

PHYSIOGNOMIC SUBCLASS — Mainly evergreen woodland

PHYSIOGNOMIC GROUP — Temperate evergreen needle-leaved woodland

FORMATION — Needle-leaved evergreen seasonally flooded/saturated woodland with rounded crowns

ALLIANCE — *Pseudotsuga menziesii* woodland

ASSOCIATION — *Pseudotsuga menziesii/Festuca idahoensis* woodland

Fig. 1. An example of the TNC terrestrial physiognomic–floristic hierarchy (Grossman et al. 1994b).

physiognomic classifications of UNESCO (1973) and Driscoll et al. (1984) and combined this with two floristic levels to create an hierarchical, physiognomic–floristic approach (Fig. 1) which is now widely used for conservation and resource planning across the United States.

The common question for terrestrial classification approaches is whether the objective is to portray existing vegetation, potential natural vegetation, or both. Classifications emphasizing existing vegetation determine vegetation units based on existing structure, composition, and successional status (Haufler 1994). Classifications emphasizing potential natural vegetation use vegetation characteristics that represent the most mature conditions of vegetation development (Küchler 1964). In the words of Tüxen (1956, in Mueller-Dombois and Ellenberg 1974), potential vegetation becomes "the vegetation structure that would become established if all successional sequences were completed without interference by man under the present climatic and edaphic conditions."

4.1.2 Zoogeographic Classification

Zoogeography is the scientific study of the distribution of animals on the earth and the mutual influence of environment and animals on each other (Allee and Schmidt 1937). It is more difficult to summarize and represent than plant geography, simply because animals are much less easily observed and are highly mobile. Approaches to zoogeography include: (1) the faunal compositions of landscapes and regions, (2) the evolutionary dynamics of the geographical ranges of animals, and (3) the mutual relationships of geographic ranges with humankind (Allee and Schmidt 1937, Muller 1974).

Classifying animals with reference to their geographic locations dates back to the first century A.D. when faunal lists were created for specific areas (cf. Allee and Schmidt 1937). Faunal classifications have focused on numerous factors, including morphological traits, geologic influences (e.g., continental drift), and ecological relationships (e.g., animal distributions seen as dependent upon localized environments, as opposed to geographic distribution and range). Regardless of emphasis, all zoogeographic approaches recognize the link between habitat and animal distributions.

As is the case for plants, animal life is unequally distributed within any zoogeographic area. Primary factors influencing the distribution of animals include (1) the means of dispersal; (2) inherent or introduced landscape barriers; (3) the degree of adaptability exhibited by the species (Allee and Schmidt 1937); and (4) competition with other species. Animal distributions are further complicated by the fact that many species (e.g., most insects, crustaceans and fishes) have several life history stages, each with its own discrete habitat. Another major complicating factor is that different taxonomic animal groups have strikingly different geographical affinities. It is possible to construct classifications for birds, mammals, and invertebrates that have only a superficial resemblance in geographic pattern of distribution to one another. Even when "hot spots" for endemic species with limited ranges are identified for conservation purposes, the resulting maps for different taxonomic groups are not well aligned (see the case of birds vs. amphibians and mammals in Bibby et al. 1992). Thus, the concept of a "formation" or "association" does not apply to fauna, except for species that are highly restricted to specific plant units at small scales. In these cases, the term "community" may be used. Additionally, the habitat requirements of most species are multi-scale in accord with differing life-history requirements, meaning that the distributions of most animals are best viewed in an hierarchical framework in which distributions at different life-history stages are dependent on sets of habitat requirements defined at those scales. For many species, the scales may vary from inter-continental during migration to highly local during reproduction.

Lawton et al. (1993) explored numerous hypotheses to describe the relationships between range sizes or distribution limits and body size, latitudinal patterns, and metapopulation theories. Multiple approaches to coarse-scale zoogeographic classification have also taken place, for example, zoogeographic realms (Muller 1974) and life zones (Merriam 1898). However,

these coarse-scale classifications are not very useful for operational land managers. Scott et al. (1993) developed a Gap Analysis approach more conducive to operational planning; it depicts species distributions based on vegetation alliances using small-scale satellite imagery. Even in this case, however, significant scale-related problems emerge.

4.2 Aquatic Classifications

As compared with terrestrial systems, aquatic systems are highly dynamic. Classification is facilitated more by abiotic than by biotic features. The water's surface also presents a screen to direct viewing by visible light. As a result, aquatic classification is much less advanced than terrestrial classification. It is apparent that aquatic classification systems should not be assumed to nest easily, if at all, into terrestrial classification systems.

As aquatic systems in general are highly dynamic and subject to intense natural perturbations, the concept of a stable "climax" has not been useful. Coastal-marine systems shed some light on the question whether classifications of existing biology or biotic potential apply to other than terrestrial systems. Valiela (1984) devoted an entire chapter to colonization and succession in marine communities; it is significant that the concept of "climax" does not appear. In fact, Peters (1976) pointed out that many properties associated with succession are tautological, creating doubt on the validity of the concept of "potential" ecosystem states.

Indeed, as any recent marine biology or oceanography text will illustrate, marine ecology is dominated by process concepts that emphasize change. Succession is seen as the composite result of a complex of factors. Perhaps it is for this reason, that few "potential" or "climax" maps equivalent to those for terrestrial vegetation exist. An exception is the work of Hayden et al. (1984), which brought together mapped classifications of coastal–biogeographic, coastal–physical, and oceanographic environments. Although there was some concurrence in the boundaries, enough differences were present to illustrate that these three approaches express different attributes.

4.2.1 Freshwater Classifications — Rivers

Approaches to classifying freshwater ecosystems range from those focusing on single physical, chemical, or biological variables to efforts using complex combinations of all three types of variables (Naiman et al. 1992, Hudson et al. 1992). However, despite many recent advances, issues related to parameterizing the many variables and physical processes involved in watershed modeling remain a major challenge for hydrologists. These include the need to deal with scaling and the linkages among hydrology, geochemistry, environmental biology, meteorology, and climatology (Hornberger and Boyer 1995).

The development of freshwater classification has occurred in phases. Early efforts to classify river systems identified whole river system types (Davis 1890, Shelford 1911). The recognition of biological zones led to a second phase of classification (Carpenter 1928, Ricker 1934). The utility of this approach was limited, however, because the classes were only applicable in basins where zoogeography, geology, and climate were held constant; biological zones could not be compared across regions (Naiman et al. 1992). The third phase, which continues to the present day, attempts to describe systems in terms of general ecosystem processes (Illies 1961). Concurrently, geomorphologists worked to describe the physics of channel formation (Horton 1945, Leopold and Wolman 1957, Strahler 1957); their findings led to a recognition of the need to consider geologic and climatic processes (Naiman et al. 1992).

The most recent efforts classify river systems within surrounding landscapes to account for the dynamics of ecosystem processes. Building on earlier work (Warren 1979, Lotspeich 1980, Lotspeich and Platts 1982), Frissell et al. (1986) applied principles of hierarchy theory to describe stream ecosystems in a watershed context. This model has two important elements. First, ecosystem processes are regionally scaled (i.e., whole stream systems are formed by climatic and geologic events), whereas variation in channel form results from more local events, such as storms and landslides. Second, large-scale processes constrain the development of small-scale stream features. In other words, the genesis of the stream system limits the range of microhabitat systems.

Much testing of hierarchical models has focused on the constraint of the upper level ecological processes on stream systems, particularly their biological composition. For example, Larsen et al. (1986) found that ecoregions corresponded to the distribution of fish assemblages in Ohio. Similar studies were conducted in Kansas (Hawkes et al. 1986), Arkansas (Rhom et al. 1987), Oregon (Hughes et al. 1987, Whittier et al. 1988), and Wisconsin (Lyons 1989). At a coarse scale, these studies showed that ecoregional classification provides a useful means to stratify variability in fish distributions (Hughes et al. 1994). However, prediction of fish species occurrence at a given site will require a classification system that accounts for local-scale habitat features that are not apparent at the regional level (Lyons 1989).

4.2.2 Freshwater Classifications — Lakes

The development of lake classification has followed a path similar to that for rivers. Typically, they have been based on single or multiple variables (Leach and Herron 1992) that generally fall into four groups: trophic or productivity levels (e.g., Hooper 1969; Shannon and Brezonik 1972), chemical and/or biological characteristics (e.g., Moyle 1956, Bright 1968), basin origin and physiographic characteristics (e.g., Hutchinson 1957, Winter 1977), and hydrologic setting (Winter 1977).

Current efforts to classify lakes relate biological composition to large-scale ecosystem processes (Tonn and Magnuson 1982; Tonn 1990; Schupp 1992). Tonn (1990) described the environmental and historical factors that determine patterns of fish biogeography and community structure in lakes as a series of filters that operate from continental to local scales. This incorporates appropriate hierarchical levels for aquatic ecosystem processes and underscores the importance of considering the interaction of zoogeography and geoclimatic factors at the higher levels of the hierarchy. Sly and Busch (1992) suggested an approach for classifying large aquatic systems based on multidimensional, geophysical parameters. This approach allows the consideration of productivity or functional performance criteria within geophysical boundaries. It also allows flexibility in identifying three-dimensional boundaries.

4.2.3 Wetland Classifications

Wetland classification became an issue in the early 20th century through efforts related to the identification of peatlands (Mitsch and Gosselink 1986). More recently, scientists and environmental regulators have developed various wetland classifications to identify and quantify areas for management and protection purposes. The goal, as stated in Cowardin et al. (1979), is to create "boundaries on natural ecosystems for the purpose of inventory, evaluation and management." Nonetheless, this classification system is a generalized "taxonomy" that is not georeferenced and that lacks three-dimensional boundaries — a much-needed extension and refinement.

Water levels dictate the type of wetland community. Wetlands usually have their water table near or above the terrestrial surface, so that the area is seasonally or permanently covered by shallow water, in which hydrophytes dominate. The water source and duration often differs for coastal versus inland wetlands. Coastal wetlands are usually located on gentle, sloping topography, and are exposed to regular, seasonal water-level fluctuations. However, abrupt, short-term changes caused by winds are common. These dynamics encourage more distinctive zonation and prevent the aging process usually found in inland wetlands (Herdendorf et al. 1986). Inland wetlands respond to rapid water-level increases from runoff, and groundwater contribution can be significant. During hot and dry periods, the survival of some inland wetland plant communities may depend on groundwater inflow. Groundwater is of lesser significance for coastal wetlands.

Wetlands are often classified according to their plant communities. For example, coastal wetlands may be referred to by a major plant species, e.g., mangrove, *Spartina*, or *Juncus*. The approach for this classification is floristic, as described above for terrestrial vegetation.

4.2.4 Estuarine Classifications

Estuaries represent important mixing zones of fresh and marine waters. They have been classified in several ways, largely by combinations of geomorphology, hydrodynamics, and geographic (climate). Pritchard (1967) recognizes five geomorphologic categories: (1) drowned river mouths, e.g., Chesapeake Bay, (2) tectonically produced, e.g., San Francisco Bay, (3) bar-built, e.g., coastal-lagoon systems of the southeastern and Gulf coasts, and (4) fjord-like, e.g., glacially overdeepened valleys along the Alaskan coast. Birdsfoot river delta or everted river mouths, e.g., the Mississippi River Delta, may be a fifth category.

The most simplistic estuarine classification is the so-called "Venice System," which classifies estuaries solely on the basis of salinity regimes (Anonymous 1959). This has long been considered an oversimplification. In contrast, estuaries may be classified hydrodynamically as: (1) stratified, (2) partially stratified or salt-wedge, and (3) completely mixed. In stratified estuaries the freshwater floats over saltwater; river influence is greater than tidal influence. Little mixing occurs, and the wedge may move far inland. In partially stratified estuaries, freshwater flow equals tidal flow as an agent of turbulence; the resultant layering may be complex. Completely mixed estuaries are vertically homogeneous, with tidal currents dominating the freshwater inflow. All these classifications are entirely physical. Bulger et al. (1993) used a principal components analysis to demonstrate that biologically relevant salinity regimes can be derived.

Geographic (climatic) classifications represent attempts to categorize seasonal effects of climate on run-off, temperature, and daylight, all of which trigger biological responses, such as migration and spawning. Runoff is especially subject to seasonal shifts. For example, in the tropics too little rainfall occurs in the

dry season for any runoff to reach coastal areas. Lagoons may become sealed by bars formed by longshore currents and quickly become hypersaline. With the onset of the rainy season, freshets break through the bars, and flush the lagoon. As a result, the lagoon may become entirely fresh. Such dynamics are important considerations for estuarine classification. Roy (1984) recognized three main estuarine types for New South Wales, Australia: (1) drowned river valley, (2) barrier, and (3) saline coastal lake, all of which evolve by processes of infilling. He documented unique biotic assemblages in each estuarine type.

4.2.5 Coastal-Marine Classifications

It has been recognized for some time that a useful ecological integrator for aquatic systems is the watershed (e.g., Sheldon 1972, Lotspeich 1980, Seaber et al. 1984). This approach may be extended into the sea as a "seashed." The advantage of using this approach is that watersheds reflect ecological properties across terrestrial–aquatic boundaries, and thus act as controls on the distribution of biological diversity. This approach is driven by multi-scale ecosystem factors, as exemplified by Lotspeich (1980); i.e., large-scale controlling forces are climate and geology, reacting forces are soils and vegetation, and the streams themselves respond to all factors of the system. Although watershed and seashed models are relatively well-developed, they are also limited by the lack of available information on ecological interactions of the coastal zone. Significant research is needed to establish ecological relationships that are useful for coastal-marine ecological classification.

Ray and Hayden (1992) adopted concepts from Seaber et al. (1984) to develop a watershed- or seashed-based classification that recognized five coastal-zone subdivisions: uplands, coastal plain, and tidelands on the terrestrial side and the shoreface entrainment volume and offshore entrainment volume over the continental shelf. Hydrological interactions are key to this system, which is specifically intended as a comparative-hierarchical classification that is adaptable to both scientific and conservation purposes. This hierarchical approach is necessary to address the many scales that are involved. For example, the ability of any location to provide suitable habitat for a diversity of species depends on an array of physical and biotic factors that vary at different temporal and spatial scales from whole ocean basins to local estuarine and freshwater tributaries. (Regional distributions of fishes have been described by Robins [1971], Robins and Ray [1986], and Robins [1992]; the multi-scale dynamics of these relationships have been examined by Ray et al. [1997].)

4.2.6 Hierarchical Approaches

The Nature Conservancy is developing an aquatic classification system to provide a framework for the inventory, identification, and characterization of the freshwater biodiversity of North America (Higgins et al. 1996). This classification is hierarchical and allows for the characterization of aquatic communities on both abiotic and biotic levels at multiple scales (Fig. 2). This approach captures information on the ecological context of community types, including physical processes. It also characterizes the physical environment, which provides an indirect way to identify community types where biological information is not sufficient (Angermeier and Schlosser 1995).

Another recent development is that of Maxwell et al. (1995), which calls for an hierarchical framework of aquatic units (Fig. 3). This system is based on the aggregation of hydrologic units and the geographic distribution of aquatic biota (particularly fish species). The system is therefore not merely typological or descriptive, but ecological. It provides insights into system dynamics and how these units may be used for management and other purposes.

4.3 Integrated Classification Approaches

The introduction to this chapter presented the overall purposes of ecological classification. From previous sections, as well as Tables 4 and 5, it is apparent that many different classifications exist. As has been emphasized previously, terrestrial classifications have dominated the field. The classifications have many properties in common, namely the organization of data into categories, which facilitates retrieval and analysis and allows comparisons among systems. Most of these systems do not share a common approach to

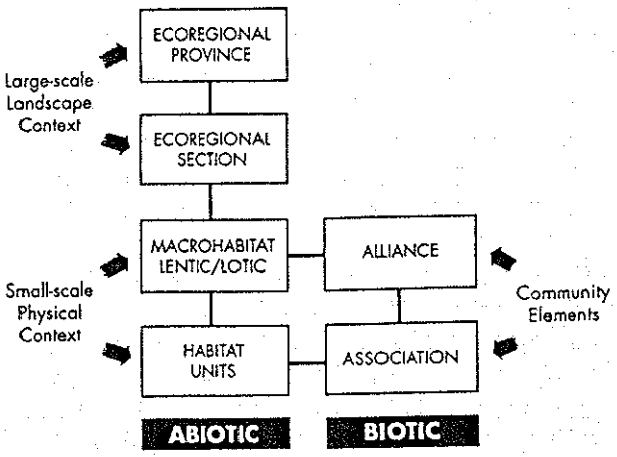

Fig. 2. TNC Aquatic Classification Hierarchy (Higgins et al. 1996).

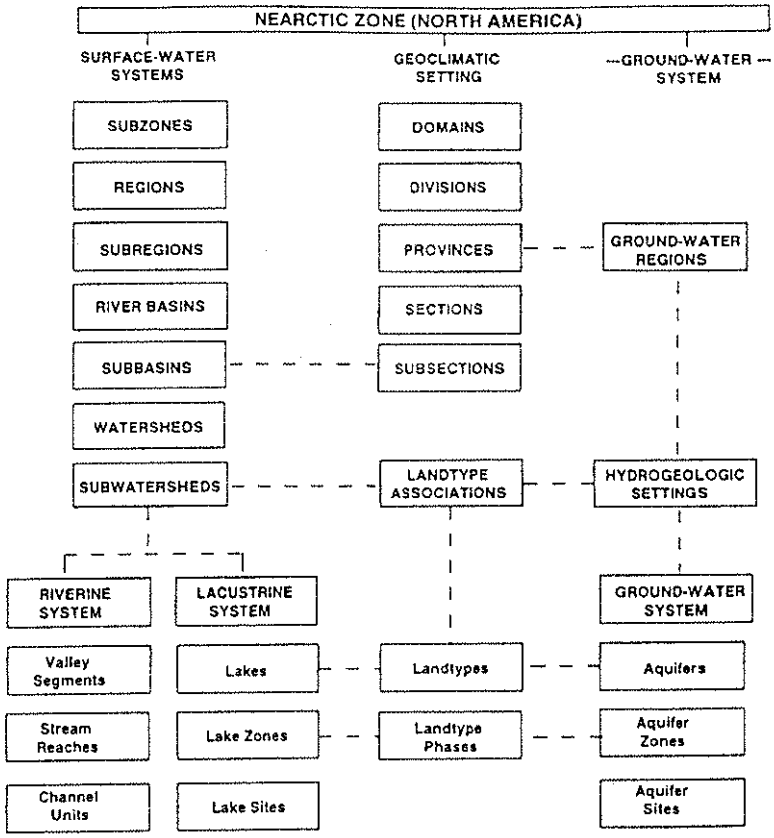

Fig. 3. US Forest Service Aquatic Ecological Unit Hierarchy (Maxwell et al. 1995).

classification, and this is of utmost importance for ecosystem management. Nor is it clear, at this point, if the different classifications may be reconciled into or around a common classification approach.

4.3.1 Site Classifications

Single Factor

Single-factor site classifications generally assume that the chosen characteristic best reflects spatial patterns of the environmental resources of interest (Omernik and Gallant 1989). For terrestrial sites, these classifications are primarily intended to reflect plant and animal potentials. Several site classification systems have used only vegetation to determine site potentials, usually with reference to successional trends or productivity. In this sense, these systems focus on potential natural vegetation (e.g., Fenneman 1946; Küchler 1967; Udvardy 1975; Brown et al. 1979, 1980). A widespread approach to site classification using vegetation is the habitat type classification system (Daubenmire 1952, Pfister and Arno 1980, Kotar et al. 1988). This system focuses on natural climax or near climax vegetation, and recognizes all understory species as a reflection of site characteristics. Relationships between vegetation and the soils or landform factors are established during and after the classification process, but these factors are not used to define the vegetation units (Komarkova 1983). The units described are natural ones, but emphasis is placed on determining vegetation units that represent "ecologically equivalent landscapes" (Kotar et al. 1988). Insofar as they describe the floristic composition of part of the natural vegetation, namely climax stands, the units of the habitat type are fairly equivalent to the plant association concept used in the western United States (Komarkova 1983). The intent is to use these descriptions to classify sites that are not at climax and, by examining their understory composition, to infer their ecological potential.

Somewhat different from the habitat type approach is the ecological species group approach, which maintains that species show similar "ecological behavior." Generally, these species belong to the same layer of vegetation (e.g., the herb layer, nonvascular layer, or shrub layer). The method presumes that communities are combinations of plant species whose composition depends on the local environment (Mueller-Dombois and Ellenberg 1974). The community unit identified can, at times, be very similar to the plant association, whereby the ecological species groups are the diagnostic species for the association. However, it is

also possible that the same association could contain several ecological species groups (Mueller-Dombois and Ellenberg 1974). The ecological species group information can either be used by itself to indicate site characteristics, in which case the system partially resembles the habitat type system, or it can be integrated with other measured site factors as part of an ecosystem classification (Pregitzer and Barnes 1982, Cleland et al. 1994).

Multiple factor

Multi-factor classifications are based on the idea that ecosystems and their components display regional patterns that are reflected in a combination of causal and integrating factors (Bailey 1983; Austin and Margules 1986; Omernik and Gallant 1987). Existing multi-characteristic frameworks include, but are not limited to, the British Columbia biogeoclimatic system (Pojar et al. 1987), Cajender's (1926) forest types, Daubenmire's (1968) habitat types, the ecoregions of the conterminous United States (Omernik 1987, Gallant et al. 1989, Omernik and Gallant 1989), Bailey's (1976, 1980) ecoregions of the United States, and the major land resource areas (USDA Soil Conservation Service 1981). Many similarities are found among these classification systems. For example, site classifications include floristic information that is collected in the same way as that which would be used for vegetation classification (Mueller-Dombois and Ellenberg 1974, Pregitzer and Barnes 1982). Similarly, habitat type classifications define plant associations in a similar manner to that of the floristic system of Braun-Blanquet. Furthermore, site classifications that bring together independent vegetation, soil, and landform classifications rely on the independent classification of these variables as their starting point (Jones et al. 1983, Sims et al. 1989, Host 1993). Site classification systems that use multiple factors subdivide land into major and minor land types or landscape ecosystems. They have been developed primarily for land managers who need to integrate resource management, biological conservation, and restoration planning. These systems are most appropriate for classifying ecosystems, which are defined by the dynamic interactions of the biotic and physical components. As with vegetation classifications, emphasis is placed on units that are more or less homogeneous both as to form and structure, but in this case with respect to all factors of the land and the vegetation (Rowe 1961).

An ecosystem approach to classification, namely that the plant community is considered together with its environment, was implicit in Clements work (1916), but was defined explicitly by Tansley (1935) and similarly by Sukachev (1945) as "biogeocoenosis." Central to the application of the approach is that all parts of the ecosystem are included. In some ecosystems, each part — vegetation, soils, climate and landform — is first studied independently and then combined (Jones et al. 1983, Driscoll et al. 1984, Sims et al. 1989). In others, the parts are combined at the outset because it is their joint interactions on the landscape that define the units. Because it is difficult to integrate multiple factors and understand their interactions beyond the local level, the units are usually considered hypotheses in need of further testing (Albert et al. 1986). Mapping is a key product from this process (Rowe 1984, Zonneveld 1989). Bailey's ecoregional map of the United States (1976, 1995) is more similar to the independent approach because Bailey relies heavily on separate climatic, physiographic, and vegetation maps and then reconciles their boundaries. The works of Albert et al. (1986) and Cleland et al. (1994) represent the combined approach.

The biogeoclimatic zone system of Krajina (1965, in Mueller-Dombois and Ellenberg 1974) is another system in which vegetation is emphasized when defining landscape or ecosystem units. These zones are defined as geographic areas that are predominantly controlled by the same macroclimate and contain similar soils and (climatic climax) vegetation. The definition of the zones at lower scales uses vegetation units that are defined by the plant association concept (Pojar et al. 1987). At higher levels, climatic zones and topographic position are used to group vegetation units into biogeoclimatic zones.

4.3.2 Ecoregional Classifications

Ecoregions are defined as geographical zones that represent groups or associations of ecosystems that function in a similar way. Ecoregions are assumed to be highly uniform with respect to their abiotic and biotic factors, the processes controlling their ecosystems, and their limits and prospects for human exploitation. Consequently, classifying the world into an organized geographic system and subdividing the earth's surface into consistent regions is difficult.

In general, two distinct concepts have been used. The first is the "controlling factor(s)" concept (Bailey 1983, 1996), in which it is assumed that one or more environmental factors act as primary controls or limitations for a particular ecoregion as defined at a particular scale. The second is the "synthesis approach" (Omernik 1987), which assumes that a holistic integration of all predominant and stable components must be considered in the regionalization. This approach defines ecoregions by perceived patterns in a com-

bination of causal and integrative factors, including land use, land surface form, potential natural vegetation, soils, and so on. The distinction between these approaches is obscured when they are mapped because mapping always requires a reduced set of differential and associated characteristics.

Through over 100 years of development of biogeography, many ecoregion systems have been produced at various scales from global to local. Many approaches and applications have been developed, including some which integrate soils, land forms, and vegetation (see Herbertson 1905, Austin 1972, Udvardy 1975, Bailey 1976, Omernik 1987, Bailey 1995). Below is a brief description of four ecoregional classification systems that are presently used in North America — two for Canada and two for the United States. Also included is a brief description of a new ecoregional classification system that was developed by the World Wildlife Fund to evaluate conservation priorities at an ecoregional level in Latin America and the Caribbean.

Controlling Factor Approaches

Ecoclimatic regions of Canada: Environment Canada has developed the "Ecoclimatic Regions of Canada, First Approximation" (1989). This is a traditional "control factor(s)" approach to creating a hierarchy of regionalizations. In order of decreasing size and generality, the map includes ecozone, ecoprovince, ecoregion, and ecodistrict levels. Climate guides the development of the ecoprovinces, although physiography, such as large mountain ranges, has major modifying influences. Ecoregions were subdivided based on the effects of macroclimate on the vegetation. Ecoclimatic regions were defined as broad areas on the earth's surface characterized by distinctive ecological responses to climate as expressed by vegetation and reflected in soils, wildlife, and water. Within ecoclimatic regions, similar trends in vegetation succession will be found on similar soils occurring on similar parent materials and positions on the landscape. Ten ecoclimatic provinces and 77 ecoclimatic regions were identified in Canada.

Ecoregions of the United States: Bailey (1976, 1980, 1983) developed a national regionalization of ecosystem units for the U.S. Forest Service. It is a hierarchical system, and similar in concept to the Environment Canada system. Four broad ecological levels (domain, division, province, section) are distinguished, based on climate and biogeography. Domains are identified by broad climatic similarity, such as lands having dry climates at the subcontinental scale. The domains are quite heterogeneous and are further subdivided into divisions through additional climatic criteria. Divisions are subdivided into provinces on the basis of the climax plant formation that geographically dominates the upland area of the province. Provinces are further subdivided into sections by differences in the composition of the climax vegetation type. The sections correspond generally to the potential natural vegetation types of Küchler (1964). As an extension of this system, an Ecological Classification and Mapping Task Team (ECOMAP), was formed in the U.S. Forest Service to develop a consistent approach to ecosystem classification and mapping at multiple geographic scales. A national hierarchical framework of ecological units was developed by the ECOMAP team with four new levels under Bailey's section: subsection, landtype association, landtype, and landtype phase (McNab and Avers 1994). ECOMAP is described in greater detail in the "Synthesis Approaches" section.

Synthesis Approaches

Terrestrial ecozones of Canada: Using the synthesis approach to integrate a different set of assumptions in mapping and characterizing regional land units, Wiken (1986) developed "Terrestrial Ecozones of Canada." Although its nomenclature is similar to that of the Ecoclimatic Regions of Canada, this system is based on predominant and stable biophysical characteristics, rather than a singular controlling mechanism. Ecozones (15 units) are areas of the earth's surface representing large and very generalized ecological units, characterized by various abiotic and biotic factors. Ecoprovinces (45 units) are parts of ecozones characterized by major assemblages of structural or surface forms, faunal realms, and vegetation, soil, hydrological and climatic zones. Ecoregions (177 units) are parts of ecoprovinces characterized by distinctive regional ecological responses to climate, as expressed by the development of vegetation, soil, water, and fauna.

Ecoregions of the conterminous United States: Omernik has produced a map entitled "Ecoregions of the Conterminous United States" (Omernik 1986, 1987) that shows 76 ecoregions at a scale of 1:7,500,000. Omernik's method grew out of an effort to create a stream classification system for the U.S. Environmental Protection Agency to plan water resource management. The premise behind Omernik's approach is that ecological regions can be identified by analyzing the patterns and composition of biotic and abiotic phenomena that reflect differences in ecosystem quality and integrity (Wiken 1986; Omernik 1987, 1995). These phenomena include geology, physiography, vegetation, climate, soils, land use, wildlife, and hydrology. The relative importance of each characteristic varies from one

ecological region to another, regardless of the hierarchical level.

ECOMAP

Until the early 1990s, no single system had been developed with the structure and flexibility needed to develop ecological units from continental to local scales.

The National Hierarchical Framework of Ecological Units (Avers et al. 1994) was developed by the U.S. Forest Service to provide a consistent, hierarchical framework for application throughout the United States. ECOMAP uses a single factor approach at some levels, and a synthesis approach at others. Because ecological variables and processes operate at different spatial spaces, each level of the hierarchy is associated with particular design criteria for its scale (see Table 1).

At the ecoregion scale, the domains, divisions, and provinces are adapted from Bailey (1980, 1995), and are recognized by differences in global, continental, and regional climatic regimes and gross physiography. These upper levels are based on regional climatic types of Köppen (1931), as modified by Trewartha (1968). In addition to climate and physiography, the units at the

Table 1. ECOMAP: Principal map units and design criteria (Avers et al. 1994).

Scale	Ecological Unit	Principal Map Unit Design Criteria*	Map Scale Range	General Polygon Size
Ecoregional	Domain	• Broad climatic zones or groups (e.g. dry, humid tropical).	1:30,000,000 or smaller	1,000,000's of square miles
	Division	• Regional climatic types (Koppen 1931, Trewatha 1968). • Vegetational affinities (e.g. prairie or forest). • Soil order.	1:30,000,000 to 1:7,500,000	100,000's of square miles
	Province	• Dominant potential natural vegetation (Kuchler 1964). • Highlands or mountains with complex vertical climate–vegetation–soil zonation.	1:15,000,000 to 1:5,000,000	10,000's of square miles
Subregion	Section	• Geomorphic province, geologic age, stratigraphy, lithology. • Regional climatic data. • Phases of soil orders, suborders or great groups. • Potential natural vegetation. • Potential natural communities (PNC) (FSH 2090).	1:7,500,000 to 1:3,500,000	1,000's of square miles
	Subsection	• Geomorphic process, surficial geology, lithology. • Phases of soil orders, suborders, or great groups. • Subregional climatic data. • PNC—formation or series.	1:3,500,000 to 1:250,000	10's to low 1,000's of square miles
Landscape	Landtype Association	• Geomorphic process, geologic formation, surficial geology, and elevation. • Phases of soil suborders, families, or series. • Local climate. • PNC—series, subseries, plant associations.	1:250,000 to 1:60,000	100's to 1,000's of acres
Land unit	Landtype	• Landform and topography (elevation, aspect, slope gradient, and position). • Phases of soil subgroups, families, or series. • Rock type, geomorphic process. • PNC–plant associations.	1:60,000 to 1:24,000	10's to 100's of acres
	Landtype Phase	• Phases of soil families or series. • Landform and slope position. • PNC—plant associations or phases.	1:24,000 or larger	< 100 acres

*Note: Criteria listed are broad categories of environmental and landscape components. The actual classes of components chosen for designing map units depend on the objectives for the map.

Table 2. Examples of subsection descriptions (Keys et al. 1996)

MAP UNIT TABLES: ECOLOGICAL UNITS OF THE EASTERN UNITED STATES -- FIRST APPROXIMATION

212A AROOSTOOK HILL AND LOWLANDS SECTION

Subsection	Geomorphology; Elevation	Quaternary geology; Stratig. & lithology	Soil taxa; Temp. & moisture regimes	Climate P(in)	Climate T(F.)	Climate Gs(d)	Potential Vegetation	Surface water characteristics	Human use
212Aa Aroostook Hills and Lowlands	Open low mountains; 200-2500 ft.	Wis. loamy-sandy loamy till; Paleozoic pelite-sandstone-conglomerate	Haplorthods, Epiaquepts, Endoaquepts; Frigid, udic, aquic	36	39	109	Sugar Maple-Birch-Beech, Red Spruce-Balsam Fir Forest, Pine-Heath Woodland	Few lakes, ponds, rivers, numerous streams	Forestry Agriculture
212Ab Aroostook Lowlands	Plains with high hills; 100-1000 ft.	Wis. loamy-sandy loamy till; Silurian pelite-sandstone-limestone	Haplaquents, Haplorthods; Frigid, udic, aquic	38	40	110	Sugar Maple-Birch-Beech, Red Spruce-Balsam Fir Forest, N. Red Oak-White Pine Forest	Numerous lakes, rivers, streams, large wetlands	Forestry Agriculture

212B MAINE-NEW BRUNSWICK FOOTHILLS AND LOWLANDS SECTION

Subsection	Geomorphology; Elevation	Quaternary geology; Stratig. & lithology	Soil taxa; Temp. & moisture regimes	Climate P(in)	Climate T(F.)	Climate Gs(d)	Potential Vegetation	Surface water characteristics	Human use
212Ba Central Maine Foothills	Low mountains; 200-1200 ft.	Wis. sandy loam till, marine deposits; Paleozoic calcareous sandstone, limestone, pelite	Borofolists, Haplorthods, Epiaquents; Frigid, udic, aquic	41	42	131	Sugar Maple-Birch-Beech, Red Spruce-Balsam Fir Forest and Wetlands, N. Red Oak-White Pine Forest	Numerous large lakes, rivers and streams, few wetlands	Forestry Agriculture
212Bb Maine/New Brunswick Lowlands	Open high hills; 100-800 ft.	Wis. loamy-sandy till, marine silt-clay; Devonian calcareous sandstone, limestone, monzonite	Epiaquents, Haplorthods; Frigid, udic, aquic	42	42	141	Sugar Maple-Birch-Beech, Red Spruce-Balsam Fir Forest, N. Red Oak-White Pine Forests, N. Cedar Limestone Woodland	Common lakes, ponds rivers, stream, and large wetlands	Forestry Agriculture

212C FUNDY COASTAL AND INTERIOR SECTION

Subsection	Geomorphology; Elevation	Quaternary geology; Stratig. & lithology	Soil taxa; Temp. & moisture regimes	Climate P(in)	Climate T(F.)	Climate Gs(d)	Potential Vegetation	Surface water characteristics	Human use
212Ca Maine Eastern Interior	Open hills; 100-800 ft.	Wis. loamy-sandy till, Devonian alkali feldspar syenite-biotite granite	Haplorthods, Epiaquents, Borosaprists; Frigid, udic, aquic	44	42	139	Sugar Maple-Birch-Beech, Maritime Red Spruce-Balsam Fir, N. Red Oak-White Pine Forests, N. Red Oak Summit Woodland	Common lakes, ponds and streams, few rivers; few, large wetlands	Forestry Agriculture Rural
212Cb Maine Eastern Coastal	Plains with hills; 100-300 ft.	Quaternary marine silt-clay, sandy loam till; Devonian gabbro diorite, monzonite diorite, quartz monzonite	Haplorthods, Epiaquepts, Endoaquods, Borofolists; Frigid, udic, aquic	47	43	152	Sugar Maple-Birch-Beech, Maritime Red Spruce-Balsam Fir, N. Red Oak-White Pine Forests, Freshwater Tidal Marsh	Coastal, saltmarsh, few lakes, ponds, rivers, streams	Rural Agriculture Recreation

Table 3. ECOMAP: National hierarchy of ecological units associated with purpose.

Planning and Analysis Scale	Ecological Units	Purpose, Objectives, and General Use
Ecoregions		
Global	Domain	Broad applicability for modeling and sampling. RPA assessment. International planning.
Continental	Division	
Regional	Province	
Subregions	Sections	RPA planning. Multi-forest, statewide, and multi-agency analysis and assessment.
	Subsections	
Landscape	Landtype Association	Forest or area-wide planning, and watershed analysis.
Land Unit	Landtype	Project and management area planning and analysis.
	Landtype Phase	

province level are further characterized and classified by soil orders and potential natural communities (from Küchler 1964).

At the subregion scale, sections and subsections are characterized by combinations of climate, geomorphic process, topography, and stratigraphy. These factors influence moisture availability and exposure to radiant solar energy, which in turn directly control hydrological function, soil-forming processes, and potential plant community distributions (Avers et al. 1994). The classification and descriptions have now been completed throughout the United States at the section level (McNab and Avers 1994). Numerous regions (the eastern United States, California, and the Columbia Basin) have completed classification, characterization, and mapping at the subsection level (see Keys et al., in press). An example of the level of detail for the map units is shown in Table 2. In the upper midwest (Minnesota, Wisconsin, and Michigan) and other areas this work has been completed to the subsubsection level (see Albert 1994).

At the landscape scale, the landtype association is defined by general topography, geomorphic process, surficial geology, soil, potential natural community patterns, and local climate (Formann and Godron 1986; Avers et al. 1994). At this level, terrestrial features and processes may also have a strong influence on ecological characteristics of aquatic habitats (Platts 1979, Ebert et al. 1991). At the land unit scale, landtypes and landtype phases are designed and mapped in the field based on properties of local topography, rock types, soils, and vegetation. These factors influence the structure and composition of plant communities, hydrologic function, and basic land-use capability (Avers et al. 1994).

Taxonomic and geographic scales: implications for classifications and their integration: The different scales inherently associated with the levels of the National Hierarchical Framework of Ecological Units have implications for the specific types of planning objectives for which each can be used. Table 3 shows the general utility of each ECOMAP level.

Biodiversity Pattern Approaches

Terrestrial ecoregions of Latin America and the Caribbean: With the objective of setting conservation priorities at an ecoregional level, the World Wildlife Fund developed a hierarchical, terrestrial ecoregion system for Latin America and the Caribbean (Dinerstein et al. 1995). This system is based on an estimation of the "original," pre-Colombian distribution of habitats in this area, and differs significantly from the approaches used in the United States and Canada. Three hierarchical levels were identified: major ecosystem types, major habitat types, and ecoregions. Major ecosystem types (5 units) are defined primarily by dynamic properties and spatial patterns of biodiversity, not wholly by vegetation structure. Major ecosystem types are subdivided into major habitat types (11 units) based on general habitat structure, climatic regimes, and major ecological processes. The level of species turnover with distance (beta diversity) is also considered, with flora and fauna showing similar guild structures and life histories. Nested within the major habitat types, ecoregions are identified to represent geographically distinct assemblages of natural communities that share a large majority of their species, ecological dynamics, and similar environ-

mental conditions. The ecological interactions critical for the long-term persistence of these communities are also considered.

4.3.3 Land Cover Classifications

Land cover classifications are primarily intended for land management or resource planning. They emphasize conspicuous features of the land surface, and can be combined with land-use maps to convey an overall perspective of what is visually perceived on the land. Many classification systems derive land cover units from general structure and composition of the vegetation (Anderson et al. 1976). For example, cover types, named by the dominant tree (Eyre 1980), are used as a descriptive land cover classification of forest lands.

Recent land cover systems have increasingly relied on factors that can be characterized through remote sensing imagery (Witmer 1978). Examples include the Gap Analysis (GAP) and the Multi-Resolution Land Characterization (MRLC) Programs. GAP is a national program that uses remote sensing to derive landcover types, which are then used to model the distribution and protection status of animal species. Similarly, the MRLC Program is creating a consistent, remote sensing-based land cover characterization approach across the nation that can be used for both one-time and repeatable resource inventory and environmental assessment objectives.

5 USE OF ECOLOGICAL CLASSIFICATION SYSTEMS

Many ecological classification systems use existing biological and environmental information to predict patterns, processes, and occurrences that will support conservation and management objectives. Classifications have been able to integrate more information in recent years, and the resulting products can increasingly be applied to multiple purposes (e.g., strategic planning, environmental monitoring, protected-area identification). Caution must be exercised, however, when using classifications and maps to make resource conservation and management prescriptions when those products were developed through combining preexisting data sets. The products derived from such integrated data sets are, as a rule, much less precise in terms of class and spatial accuracy than their component parts.

Care must be taken to develop classifications tailored to their intended applications and to choose the most appropriate classifications for addressing specific management needs.

5.1 Data Issues

Four questions relating to data need to be addressed when developing an ecological classification system: (1) what kind of data are needed, (2) how many data are needed, (3) can existing data be used, and (4) what are the costs associated with preparing data for the classification system? All four questions must be answered in relation to the specific management objective(s) to be addressed.

To respond to the first two questions, it must be recognized that the different applications of ecological classification may not necessarily be achievable through the use of one data set or analysis. Characterization data are used grouping similar patterns and delineating areas of interest. Pattern recovery data are used to extrapolate or interpolate the classification units to areas that have not been sampled. The amount of data needed to satisfy either of these applications is related to the required accuracy and precision of the classification system. Additional data may be needed to characterize the properties of each classification unit. Therefore, the total amount of data needed depends on the objective of the classification; the required accuracy and precision for pattern characterization and recovery; and the type of description required for each classification unit.

To answer the third question, it is important to determine what types of data are already available and whether they will be useful and cost effective before undertaking original research. Existing data sources may include remote sensing imagery, herbarium and museum species records, and plot/transect data that have been collected during past ecological surveys. Data, maps, and charts for vegetation, soils, lakes, geology, fresh waters, estuaries, salinity, temperature, coastal geomorphology, and climate also exist in many geographical areas. Because using existing data often involves compiling disparate and interdisciplinary data, problems related to differences in sampling dates and design, data quality and storage, spatial representation and resolution, and standardization must be solved (see Davis et al. 1991, Davis 1995). Nevertheless, existing data that are well organized and appropriate to the objective can, in certain instances, be an effective way to help develop ecological classifications and maps (e.g, Reid et al. 1995).

The fourth question, regarding costs, can only be answered following the first three. Cost is determined by the amount of equipment, techniques, skills, and time necessary to acquire the type and amount of data needed. It should be noted that, although it might be more expensive, it is often easier to build ecological classifications and prepare maps using new data,

rather than attempting to derive them from existing products and data. An example of this concerns the high costs and questionable utility of digitizing old maps of undocumented spatial accuracy into geographic information systems (GIS).

5.2 Ecological Classification and Mapping

The relationship between classification and mapping is often confusing for scientists and managers alike. In its purest form, ecological classification is independent of mapping. It is a scientific process of methodically arranging units of quantitative information into classes or groups that possess common properties. Mapping is a representation of these units which is constrained by the scale of the map and by the spatial information that must be related to the ecological units. Additional complexity is introduced with the interpretation of "spectral signatures" or an aggregation of available georeferenced "data layers."

Maps will never exactly represent ecological units unless those units were developed through the aggregation of spatial thematic layers. A map of earth cover that is created through the analysis of remotely sensed data or interpretation of aerial photography will not portray an ecological classification system. If cover types are determined to be an important factor of an ecological classification system, additional research must be conducted to define the relationship between the cover classes and the ecological classification units.

As reviewed earlier in this chapter, ecological classifications may be developed by using a variety of variables. Using spatial data (maps) that include variables needed for a classification system can greatly simplify the process of creating an ecological classification map. Spatial data sets have variable thematic and locational accuracy, so that when a map is compiled from multiple spatial products, its overall accuracy is unpredictable and interpretation must be tentative. Furthermore, the boundaries of separate map themes rarely coincide, largely because of real differences among attributes. This is as true for land units (Bailey et al.1994), as it is for coastal (e.g., physical vs. biogeographic units), and marine units (e.g., marine phytoplankton vs. physical oceanographic regimes (McGowan 1972, Hayden et al. 1984).

In addition to these technical challenges, care must be taken not to substitute a composite map of ecological components for a map of ecological units. Overlay maps do not represent the ecological relationships between the individual layers. An ecological unit in the natural environment is not merely a compilation of independent components, but is functionally integrated.

5.3 Ecological Boundaries: What Do the Lines on Maps Mean?

Ecological variables are generally semi-continuous, as opposed to being categorical, and are expressed as gradients. The concept of the "ecotone" reflected this (di Castri et al. 1988, di Castri and Hansen 1992): "...the ecotone is a 'zone of transition' between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales, and by the strength of the interactions between adjacent ecologic systems." Ecotones may be expressed at any scale. As a result, distinct lines between ecological units are the exception rather than the norm.

The problem of where to draw a line on a map is complex and requires an explicit set of rules and disclaimers. Two untested assumptions are typically made: (1) the mappable attribute is a clearly defined and a predictable property of the ecological unit, and (2) the mappable attribute does not vary over the known distribution range of the ecological unit (Bourgeron et al. 1993). This is difficult enough for simple variables, but when multiple variables are brought into the classification framework, the "fuzziness" of the lines increases dramatically.

Consequently, several important factors must be considered when developing a map of ecological units. First, interpreting ecological units depends in part on knowledge of the distributions of environmental attributes along gradients. Second, the ecological relations among biotic and abiotic components need to be stated and tested explicitly. A clear link between scales, patterns, and processes must be established, and temporal variability must be considered (Bourgeron et al. 1993). The question becomes how much fuzziness in the transition zone is acceptable to meet the classification and mapping objectives. Strategic planning may tolerate more fuzziness, whereas operational planning typically tolerates less. Regardless of the management needs, any ecological map must produce boundaries that are ecologically significant. One way to become explicit is to map the gradients themselves.

The concept of ecoregions is intuitively attractive for all systems — terrestrial, freshwater, and marine. The reconciliation of boundaries among different environmental attributes, as has been done for terrestrial systems (e.g., Bailey 1995), remains problematic. Ecological classifications, especially when presented on maps, give the appearance of ecosystem stasis and offers few opportunities for further analysis.

Furthermore, when classification approaches are dominated by few factors, they tend to address some systems better than others. Each environmental factor and/or system exhibits its own behavior, which in

mapped terms may be expressed as gradients across the land- or seascape. Combining these may be possible only through statistical modeling approaches of "dynamic biogeography" (e.g., Hengeveld 1990). The science of ecosystem classification and geography still has a long way to go, especially in the "critical areas of treatment of heterogeneity and scaling" (Hornberger and Boyer 1995).

5.4 Key Attributes of Representative Classification Systems

Forty-four classification systems are presented in Table 5, and key attributes in six topic areas are listed for each system. The table can be used to evaluate what each effort classifies (e.g., terrestrial vs. freshwater systems), how the classification was developed (e.g., use of abiotic vs. biotic factors), and at what scale the system is classified (e.g., global vs. local). One classification system often addresses more than one attribute in a topic area; for example, that of Grossman et al. (1994b), Grossman et al. (1998) considers both terrestrial and wetland systems. Each classification effort is described by:

- The ecological system that the effort classifies — terrestrial, freshwater, coastal/marine, estuarine, and/or wetland;
- The geographical coverage that the effort encompasses —global, continental, national, regional, and/or local;
- The overall objectives of the classification effort — research, management, and/or conservation;
- The environmental factors used to develop the classification effort — climate, soils, elevation, geology, landform/land position, and/or hydrology/hydrography;
- The biological factors used to develop the classification effort — existing vegetation structure, existing vegetation composition, potential natural vegetation, zoological guilds, and/or zoological composition; and,
- Other factors that are important in describing the classification effort, such as: are the classification units geographically referenced? Is the classification hierarchical (i.e., do multiple levels exist)? Were a variety of factors used to develop the classification effort? Were extensive data needed to develop the classification?

5.5 Management Applications

Regulatory and management agencies at all levels of government, have struggled to apply ecological classifications to resource planning and management challenges. The diversity of ecological classifications has been reviewed in earlier sections. Each system has been developed for a specific set of purposes and many have proven extremely valuable for management applications (see Management Chapter). However, having value for one set of applications does not make a classification system useful for other applications. For example, classification systems that focus on site potential (e.g., ECOMAP Land Type Associations) may be appropriate for gross, strategic analyses of resource management. For operational planning or statistically defensible estimates, analyses that are conducted at the stand level and that integrate existing and potential vegetation are recommended (Roloff 1994).

Table 6 provides an evaluation of the applicability of the major ecological classification systems for different management applications. The management applications are divided into four general areas: land management and use, biodiversity conservation, resource inventory and management, and research and assessments. Additional discussion concerning the applications of ecological classification systems to meet management objective can be found in Carpenter et al. (this volume).

"Land management and use" activities focus on the land unit and its development by humans for a variety of purposes, including

- Infrastructure siting for roads and other "conduits" and buildings;
- Resource planning, site prescription, and management for forestry, wildlife, fisheries, recreation, agriculture, erosion control, minerals and water, and multiple use designations;
- Desired future conditions analysis; and
- Sustainable development.

"Biodiversity conservation" refers to the identification and protection of natural biota as it occurs in ecological systems, including:

- Biological diversity inventory;
- Identification of conservation sites;
- Sustainable design for conservation; and
- Restoration planning.

"Resource inventory and management" includes activities intended to determine the existing number, abundance, and condition of natural resources to

Table 5. Key attributes of major ecological classification efforts (under development).

	Ecological System					Geographical Coverage					Objectives			Environmental Factors						Biological Factors					Other Factors			
Classification Effort	Terrestrial	Freshwater	Marine/Coastal	Estuarine	Wetland	Global	Continental	National	Regional	Local	Research	Management	Conservation	Climate	Soils	Elevation	Geology	Landform/Position	Hydrology/Hydrography	Existing Vegetation Structure	Existing Vegetation Composition	Potential Natural Vegetation	Zoological Guilds	Zoological Composition	Classification Units Are Geographically Referenced	Hierarchical (multi-level)	Multi-factored	Extensive Data Requirements
Albert et al. (1995)	√				√				√		√			√	√	√	√	√	√			√			√	√	√	
Allee and Schmidt (1937)	√								√		√			√									√	√	√			
Anderson et al. (1976)	√							√				√									√					√		√
Bailey (1995)	√	√	√		√	√	√	√	√		√	√		√		√		√				√			√	√	√	
Braun-Blanquet (1928, 1932)	√				√	√					√										√					√		
Busch and Sly (1992)		√				√					√	√							√				√	√			√	
Cleland et al. (1994)	√				√				√	√	√	√		√	√	√	√	√	√			√			√	√	√	
Cowardin et al. (1979)		√		√	√			√			√	√			√				√		√				√	√	√	
Daubenmire (1952)	√				√						√				√			√			√						√	
Dinerstein et al. (1995)	√				√		√		√			√	√							√	√	√			√	√		
Driscoll (1984)	√				√			√	√			√		√						√	√							
ECOMAP (1993)	√				√			√	√	√	√	√		√	√	√	√	√	√			√			√	√	√	
Ecoregions Working Group (1989)	√							√			√	√		√	√	√		√		√		√			√	√		√
Frissell et al. (1986)		√									?								√							√		
GAP/Scott et al. (1993)																												
Grossman et al. (TNC) (1994)	√							√				√	√	√	√		√	√		√	√					√		
Hayden et al. (1984)			√								?		√						√							√		
Higgins et al. (TNC) (in prep)		√						√				√	√				√	√	√	√	√		√	√		√		
Holdridge (1947)	√					√					√			√														
Illies (1961)		√				√					√								√						√			
Ketchum (1972)			√			√					√	?						√	√						√		√	
Kotar et al. (1988)	√									√		√										√					?	

Table 5 (continued)

Classification Effort	Ecological System					Geographical Coverage					Objectives			Environmental Factors						Biological Factors					Other Factors			
	Terrestrial	Freshwater	Marine/Coastal	Estuarine	Wetland	Global	Continental	National	Regional	Local	Research	Management	Conservation	Climate	Soils	Elevation	Geology	Landform/Position	Hydrology/Hydrography	Existing Vegetation Structure	Existing Vegetation Composition	Potential Natural Vegetation	Zoological Guilds	Zoological Composition	Classification Units Are Geographically Referenced	Hierarchical (multi-level)	Multi-factored	Extensive Data Requirements
Krajina (1965)	√					?					√			√	√	√	√					√				√	√	
Kuchler (1964)	√					√	√	√			√	√		√	√			√				√			√	√	√	
Maxwell et al. (1995)		√					√					√							√						√	√		
Mitsch and Gosselink (1986)					√			?				√			√				√	√	√						√	
MLRC (n.d.)																												
Moyle and Ellison (1991)		√			√					√		√		√				√	√	√	√					√	√	
NAWQA (1990)		√						√				√							√						√			
Omernik (1995)	√						√	√				√		√	√		√		√	√					√		√	
Pfister and Amo (1980)	√								?		?	?		√	√							√			√	√		
Pregitzer and Barnes (1982)	√									√	√	√		√	√		√	√	√			√			√	√	√	
Pritchard (1967) and Barnes (1967)				√				?									√	√	√									
Ray and Hayden (1992)			√	√					?				√						√									
Robins (1992)			√	√															√									
Rodwell (1991)	√							√			√	√									√							
Rowe (1984)	√							√						√							√				?	?		
Schupp (1992)		√								√									√					√			√	
Specht et al. (1974)	√							√				√	√	√	√		√	√		√	√					√		
Udvarty (1974)	√					√					√	√		√	√		√			√					√	√		
UNESCO (1973)	√					√					√	√		√	√		√	√		√	√	√			√	√		
USGS (1982)		√						√			√	√						√	√						√	√		
Wiken (1986)	√							√				√		√	√	√	√		√	√	√	√			√	√		
Zonneveld (1989)	√							?			√	√		√	√			?				√			√			

Table 6. Management applications of major ecological classification efforts (under development).

Classification Effort	Land Management and Use				Biodiversity Conservation				Resource Inventory and Management				Research and Assessments				
	Infrastructure siting	Resource planning, site prescription and management	Desired future conditions analysis	Sustainable development	Biodiversity inventory	Identification of conservation sites	Sustainable design for conservation	Restoration planning	Resource inventory	Resource management	Habitat suitability analysis	Resource reporting and mapping	Environmental impact assessments	Ecosystem and landscape monitoring	Study of pattern and process in relation to scale	Representativeness assessment	Predictive modeling
Albert et al. (1995)	√								√	√	√	√		√	√		√
Allee and Schmidt (1937)	√				√												√
Anderson et al. (1976)	√								√	√		√	√				
Bailey (1995)	√	√	√	√					√	√	√	√			√	√	
Braun-Blanquet (1928, 1932)																	
Busch and Sly (1992)		√							√								
Cleland et al. (1994)	√								√	√	√		√	√			
Cowardin et al. (1979)	√	√		√					√	√	√						
Daubenmire (1952)																	
Dinerstein et al. (1995)					√	√											
Driscoll (1984)	√			√													
ECOMAP (1993)	√	√		√					√	√	√						
Ecoregions Working Group (1989)	√								√	√							
Frissell et al. (1986)																	
GAP/Scott et al. (1993)																	
Grossman et al. (TNC) (1994)						√	√										
Hayden et al. (1984)						√											
Higgins et al. (TNC) (in prep.)						√	√										
Holdridge (1947)	√															√	
Illies (1961)																	
Ketchum (1972)																	
Kotar et al. (1988)									√	√	√						

Table 6 (continued)

Classification Effort	Land Management and Use				Biodiversity Conservation				Resource Inventory and Management				Research and Assessments				
	Infrastructure siting	Resource planning, site prescription and management	Desired future conditions analysis	Sustainable development	Biodiversity inventory	Identification of conservation sites	Sustainable design for conservation	Restoration planning	Resource inventory	Resource management	Habitat suitability analysis	Resource reporting and mapping	Environmental impact assessments	Ecosystem and landscape monitoring	Study of pattern and process in relation to scale	Representativeness assessment	Predictive modeling
Krajina (1965)																	
Kuchler (1964)																	
Maxwell et al. (1995)	√								√	√							
Mitsch and Gosselink (1986)																	
MERC (n.d.)																	
Moyle and Ellison (1991)					√	√											
NAWQA (1990)	√												√	√			
Omernik (1995)	√								√	√			√				
Pfister and Amo (1980)									√	√	√						
Pregitzer and Barnes (1982)									√	√	√						
Pritchard (1967) and Barnes (1967)																	
Ray and Hayden (1992)					√												
Robins (1992)									√	√							
Rodwell (1991)																	
Rowe (1984)									√	√							
Schupp (1992)									√	√	√						
Specht et al. (1974)					√	√											
Udvarty (1974)					√	√											
UNESCO (1973)																	
USGS (1982)																	
Wiken (1986)	√	√		√					√	√	√	√				√	
Zonneveld (1989)																	

inform management decisions. These activities include:

- Resource sampling;
- Resource inventory;
- Resource management — forestry, wildlife, fisheries, agriculture, recreation, soil, and minerals and water;
- Habitat suitability analysis; and
- Resource reporting and mapping.

"Research and assessments" include the evaluation and prediction of the effects of natural and human changes on natural resources and systems, including:

- Environmental impact assessments;
- Ecosystem and landscape monitoring;
- Study of pattern and process in relation to scale;
- Representativeness assessment; and
- Predictive modeling.

Perhaps the most common application of terrestrial vegetation and site classifications is the determination of appropriate uses for agricultural and forest lands. Integrated units derived from climatic, soil, and vegetation provide a useful tool for the determination of site potential. In addition, the combination of existing and potential vegetation classifications have been used to describe current conditions, predict successional processes, and characterize disturbance regimes (Haufler 1994, Roloff 1994). The limited degree of success using exclusively potential vegetation in accomplishing these goals is based on limited knowledge concerning vegetation–site relationships, and the ability of the dependence on the observers to infer site characteristics from the vegetation.

A standard application for ecological classification systems, terrestrial and aquatic alike, is conservation planning. Ecological classifications have been used extensively to inventory and protect terrestrial and aquatic areas. A direct biological classification will always provide the greatest confidence of capturing the conservation target, but coarser biological and site classifications can be used to develop a high degree of predictive accuracy. Vegetation classifications have been the primary approach for the identification and delineation of terrestrial conservation sites by resource management agencies (Scott et al. 1993, Grossman et al. 1994a). Aquatic researchers and managers have attempted to classify standardized descriptors for habitat sub-units for conservation planning (Busch and Sly 1992). Boundary delineations alone are often used in terrestrial and aquatic systems to protect delineated habitat units that are in short supply, unique, or support known species of special interest.

Especially for terrestrial systems, classifications have been developed to identify boundary conditions which can be employed to impose restrictions on land use. For wetlands connected to larger aquatic systems, the boundary between vegetated and non-vegetated areas is of considerable management interest. The federal government has the mandate to monitor wetland condition and abundance in relation to defined levels for healthy ecosystems and abundant fish and wildlife resources. Wetland classification is the first step in identifying these areas for inventory and management; subsequent steps include protection, regulation, evaluation, restoration, and rehabilitation.

Ecological classification has assisted aquatic ecosystem management in several areas, including water quality assessment (Meador et al. 1993, Paulsen and Linthurst 1994), fish productivity modeling (Fausch et al. 1988), fish habitat requirement modeling (Nelson et al. 1992, Hill and Platts 1995), and adjacent land management (Platts 1980, Maxwell et al. 1995). Because of the complexity of lakes and their typically large size, as well as the historical focus on fisheries management, classification for productivity has received considerable attention.

One example of aquatic ecosystem management is the National Water Quality Assessment Program (NAWQA). In 1990, the U.S. Geological Survey (USGS) initiated this Program as a comprehensive survey of the status and trends of ground and surface water quality in the United States. Physical, chemical, and biological data are being collected from study areas that correspond to hydrologic units based on the drainages of major rivers and aquifers (USGS 1982), which will be further stratified according to the classification framework of Frissell et al. (1986) (Meador et al. 1993). NAWQA researchers are currently assessing the use of ecoregions as a stratification tool for national sampling (J. Higgins, pers. comm.).

For wetlands, management initially focused on waterfowl and furbearer production, which had profound implications for wetland classification. In the past two decades, however, other services provided by wetlands, such as biological functions, habitat, sanctuaries, hydrological functions, and cultural values, have been identified (Greeson et al. 1979, Reppert and Sigleo 1979, Tiner 1984). In addition, society often assigns shoreline marshes a higher ecological value than other types of wetlands because of their direct contribution to fish and wildlife populations, rather than their role in larger ecosystems (Maltby et al. 1983). Estuarine wetlands and wetlands located at river mouths are also highly valued by society because wildlife (bird) and fish usage is usually high, rare plants

or unusual wildlife colonies may occur, and these areas are often near urban centers (Crispin 1990).

Descriptive attributes have been used to develop a "taxonomy" of coastal wetlands, including vegetation, hydrology, geography, climate, soils, stratigraphy, and landscape position (topography, aspect, slope). Functional attributes are also used as insights into system dynamics and management, including species life histories, multi-species interactions, landscape interactions, hydrological processes (flood storage and storm-flow modification), nutrient retention and transformation, sediment and toxicant trapping, and sediment stabilization. Both sets are then modeled to provide decisions on wildlife habitat and public use (James E. Perry, Virginia Institute of Marine Sciences, pers. comm.).

Estuaries represent high levels of complexity and conservation urgency. They house major fish populations, and provide vital habitat for early life-history stages of many marine fishes and invertebrates. All anadromous and catadromous fishes must cross estuaries. Estuaries are the sites of most of the world's large cities and ports, and also provide important industrial and commercial sites. As a result, they are centers for coastal pollution and are, in general, heavily disturbed, which has implications for coastal living resource and fishery sustainability. Classification of estuaries requires information on where various types of habitats occur, which are the best examples, and what activities most threaten them.

6 PRESENT SITUATION AND FUTURE VISION

The understanding of ecological dynamics at the community, landscape, and ecosystem levels is undergoing rapid growth. Spatial and temporal organization and dynamics are better understood through the application of hierarchy theory and remotely-sensed information. Biogeographic and environmental information are being developed at an unprecedented rate and with a high level of quality control. Technological advances in the management and analysis of spatial data are increasingly available to managers and scientists. This remarkable progress provides a suite of new opportunities for the science and application of ecological classification.

6.1 Existing Ecological Classifications

Many ecological classification systems have already been developed. Accounts of the development and application of biogeographic and ecological characterizations and classifications are abundant throughout the scientific literature. However, the existing systems do not fully meet the current expectations or needs of resource managers.

Most ecological classifications have been descriptive and have focussed on either terrestrial, freshwater, coastal, or marine systems. Up to now, terrestrial systems have dominated ecological classification efforts; these generally do not incorporate adequate information on aquatic systems (e.g., Avers et al. 1994, Bailey 1995). This is partially an artifact of traditional training in ecology and resource management, but also reflects the variable status of data and knowledge associated with the different systems.

Aquatic classifications have primarily been based on biophysical factors, whereas most terrestrial classifications emphasize vegetation (potential and existing), climate, and physiography. For example, Cowardin et al. (1979) focus on wetland topography, while Bailey (1995) emphasizes phytogeography and climate. Coastal classifications are often approached with a more comprehensive "ecosystem" perspective as they include components of both terrestrial and aquatic systems.

The increased need for sound management of natural resources and prioritization of conservation action has resulted in an increased dependence upon existing ecological classification systems. The existing ecological classification systems can address some, but not all, management and conservation concerns. Each system was developed to address a specific set of objectives. It is important to understand the intended and appropriate uses for each classification system and its associated products. No individual system will ever meet the full spectrum of potential applications.

6.2 The Development of New Ecological Classifications

Existing classifications provide the framework to go beyond mere description of the distribution of biological species and communities to focus on their relationships to one other and to environmental gradients. There are many challenges associated with the development of the next generation of classification systems.

The dynamics of environmental change are central to the concept of the ecological unit. However, it has been difficult to apply ecosystem concepts and practices to most ecological classification systems, as few of them emphasize ecological process and the dynamics of change. In addition, ecological classifications must reflect our increasing knowledge about the biological and ecological processes that function-

ally integrate terrestrial, freshwater, and coastal/marine systems. Marine classification must integrate the coastal systems which, in turn, must integrate terrestrial systems. Until more classifications integrate aquatic and terrestrial features and processes, they cannot be seen as truly "ecosystemic" and they will be restricted in applications and future value.

6.2.1 A Set of National Ecological Units

Many managers would derive great benefit from access to one common ecological classification system with explicit standards and application guidelines. In many cases, access to one standard framework of classification units would represent the most efficient and cost-effective solution to many shared resource management challenges.

The successful development of a common set of ecological units will require sufficient consensus on common objectives, appropriate scales of analysis, and the critical ecological processes and biophysical variables that function at those scales. This system ideally would integrate across multiple scales, multiple factors, and be relevant for terrestrial, freshwater and coastal/marine systems. The development of this common ecological framework would not restrict the development or use of other systems that better address specific needs and applications.

This concept of a common set of ecological units has already gathered momentum. In December 1995, a Memorandum of Understanding (MOU) was signed by the U.S. Department of Agriculture (Natural Resources Conservation Service, Forest Service, and Agricultural Research Service), the U.S. Department of the Interior (Bureau of Land Management, Geological Survey, Fish and Wildlife Service, National Biological Service, and National Park Service), and the U.S. Environmental Protection Agency. This MOU was designed to develop a spatial framework of ecological units for the United States. A National Interagency Steering Committee and a National Interagency Technical Team have been established to implement this MOU. As part of the initial and ongoing effort, maps of common ecological units will be developed and published at standard scales. Digital data sets in formats meeting available Federal Geographic Data Committee standards will also be published.

6.2.2 User-Defined Classification Systems

The quantity and quality of ecological and biological data has dramatically increased over the past few decades. More and more of these data are geographically referenced, allowing the information to be represented and interpreted spatially. Simultaneously, there have been remarkable advances in the technological capabilities for managing, aggregating, analyzing, and portraying these data. These advances have stimulated rapid testing, refinement and implementation of numerous classification and assessment approaches that are used to address various conservation and management objectives, as well as basic research questions.

This increased capacity to integrate information for targeted application will greatly augment the development of a common classification approach. Specific classifications can be developed to address specific resource management and conservation objectives. Users can determine the appropriate scales for analyses and identify the specific biophysical variables and ecological processes that apply to their specific questions and objectives. They can draw from multiple data sources to compile and analyze the appropriate spatial data and to develop very specific solutions to their questions.

Where multiple approaches to ecological classifications are appropriate, the ability to share standardized data layers becomes increasingly important. For this to occur, standards for ecological inventory, data management, and analytical approaches must be developed and documented. Ecological classifications and associated products (e.g., keys, assessments, maps, etc.) should be accompanied with appropriate metadata that fully disclose the methods, data sets, scales, variables, analyses, classes, and other information required to fully interpret the utility of the product. All data and data products must meet minimal standards so that they can be broadly interpreted and applied to multiple objectives. Data standards and inclusion of metadata files will allow partners to confidently assess the appropriateness of the data products for addressing their individual objectives.

It is critical that resource managers, conservationists, and researchers will be able to use the information. Potential users will need to have the ability to access all data so they may identify the appropriate information and ecological classification systems that would help them meet their specific objectives. This will also require a high level of terminological consistency; working definitions must be widely agreed upon and implemented to guard against inappropriate applications and faulty interpretation of ecological data, classifications, and associated products.

6.3 Human Factors

Many appropriate applications of ecological classification systems have been identified in this report, but

perhaps the most important objective for these ecological classification systems has not been specifically mentioned: the ability to use these systems for the purposes of education and communication. Ecological classification systems help managers of ecological systems understand the functions and processes of these ecosystems. This is an important step in breaking the cycle of managing for one component of an ecosystem at a time. Ecological classification systems and associated products can also provide invaluable communications tools conveying critical land management and conservation information to the general public.

Finally, ecological classification efforts have historically avoided the integration of the human dimension into the system, even as reported system attributes. Management and conservation is a human endeavor and people have an increasingly profound impact on the structure and function of ecological systems. Therefore, it is critical that we learn how to integrate key social aspects of politics, economics, anthropology, and sociology into future ecological classification efforts.

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REFERENCES

Albert, D.A. 1994. Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. Fourth revision. USDA Forest Service General Technical Report NC-178, North Central Forest Experiment Station, St. Paul, MN.

Albert, D.A., S.R. Denton, and B.V. Barnes. 1986. *Regional Landscape Ecosystems of Michigan*. University of Michigan, School of Natural Resources, Ann Arbor, MI.

Allee, W.C., and K.P. Schmidt. 1937. *Ecological Animal Geography*. Wiley, New York, NY.

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

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

Anderson, J.R., E.E. Hardy, and J.T. Roach. 1976. Land use and land cover classification system for use with remote sensing data. Geological Survey Professional Paper 964 (a revision of the land use classification system as presented in U.S. Geological Circular 671), U.S. Government Printing Office, Washington, D.C.

Angermeir, P.L., and I.J. Schlosser. 1995. Conserving aquatic biodiversity: beyond species and populations. *American Fisheries Society Symposium* 17402–17414.

Anonymous. 1959. Symposium on the classification of brackish waters. Venice, Italy, April 8–14, 1958. *Archivio di Oceanografia e Limnologia*, Volume 11, Supplemento.

Arno, S.F., and G.E. Gruell. 1985. Douglas-fir encroachment into mountain grasslands in southwestern Montana. *Journal of Range Management* 39: 272–276.

Austin, M.E. 1972. Land resource regions and major land resource areas of the United States. *Agricultural Handbook 296*. Revised edition. USDA Soil Conservation Service, Washington, D.C.

Austin, M.P. 1985. Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics* 16: 39–61.

Austin, M.P. 1987. Models for the analysis of species response to environmental gradients. *Vegetatio* 69: 35–45.

Austin, M.P. 1991. Vegetation theory in relation to cost-efficient surveys. pp. 17–22. In: C.R. Margules, and M.P. Austin (eds.), *Nature Conservation: Cost Effective Biological Surveys and Data Analysis*. CSIRO Publishing, Collingwood, Vic. Australia.

Austin, M.P., R.B. Cunningham, and P.M Fleming. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve fitting procedures. *Vegetatio* 55: 11–27.

Austin, M.P., and C.R. Margules. 1986. Assessing representativeness. pp. 45–67. In: M.B. Usher (ed.), *Wildlife Conservation Evaluation*. Chapman and Hall, London, UK.

Austin, M.P., and T.M. Smith. 1989. A new model for the continuum concept. *Vegetatio* 83: 35–47.

Austin, M.P., and G.A. Yapp. 1978. Definition of rainfall regions of southeastern Australia by numerical classification methods. *Archiv fur meterologie, Geophysik und Bioklimatologie, Series B*, 26: 121–142.

Avers, P.E., D.T. Cleland, W.H. McNab, M.E. Jensen, R.G. Bailey, T. King, C.B. Goudney, and W.E. Russell. 1994. National hierarchical framework of ecological units. USDA Forest Service, Washington, D.C.

Bailey, R.G. 1976. Ecoregions of the United States (map, scale 1: 7,500.000). USDA Forest Service, Intermountain Region, Ogden, UT.

Bailey, R.G. 1980. *Descriptions of the Ecoregions of the United States.* USDA Forest Service Miscellaneous Publication 1391, Washington, D.C.

Bailey, R.G. 1983. Delineation of ecosystem regions. *Journal of Environmental Management* 7: 365–373.

Bailey, R.G. 1989a. Ecoregions of the continents (map, scale 1: 30,000,000). USDA Forest Service, Washington, D.C.

Bailey, R.G. 1989b. Explanatory supplement to the ecoregions map of the continents. *Environmental Conservation* 15: 307–309.

Bailey, R.G. 1995. Description of the ecoregions of the United States (with separate map at a scale of 1: 7,500,000). USDA Forest Service Miscellaneous Publication 1391 (revised), Washington, D.C.

Bailey, R.G. 1996. *Ecosystem Geography.* Springer-Verlag, New York, NY.

Bailey, R.G, P.E. Avers, T. King, and W.H. McNab (eds.). 1994. Ecoregions and subregions of the United States (map, scale 1: 7,500,000). USDA Forest Service, Washington, D.C.

Bailey, R.G., and H.C. Hogg. 1986. A world ecoregions map for resource reporting. *Environmental Conservation* 13: 195–202.

Bailey, R.G., M.E. Jensen, D.T. Cleland, and P.S. Bourgeron. 1993. Design and use of ecological mapping units. pp. 105–116. In: M.E. Jensen, and P.S. Bourgeron, editors. Eastside forest ecosystem health assessment. Volume II. Ecosystem management: principles and applications. USDA Forest Service General Technical Report PNW-318, Pacific Northwest Research Station, Portland, OR.

Barnes, B.V. 1984. Forest ecosystem classification and mapping in Baden-Wurttemberg, West Germany. pp. 49–65. In: Forest land classification: Experience, problems, perspectives. *Proceedings of the symposium: March 18–20, 1984, Madison, WI, USA.*

Barnes, B.V., K.S. Pregitzer, T.A. Spies, and V.H. Spooner. 1982. Ecological forest site classification. *Journal of Forestry* 80: 493–498.

Bibby, C.J., N.J. Collar, M.P. Crosby, M.F. Heath, Ch. Imboden, T.H. Johnson, A.J. Long, A.J. Stattersfield, and S.J. Thirgood. 1992. *Putting Biodiversity on the Map: Priority Areas for Global Conservation.* International Council for Bird Preservation (ICBP), Cambridge, UK.

Borhidi, A. 1991. *Phytogeography and Vegetation Ecology of Cuba.* Akademiai Kiado, Budapest. 858 pp.

Bourgeron, P.S., H.C. Humphries, R.L. DeVelice, and M.E. Jensen. 1993. Ecological theory in relation to landscape evaluation and ecosystem characterization. pp. 65–79. In: M.E. Jensen, and P.S. Bourgeron (eds.), Eastside Forest Ecosystem Health Assessment. Volume II. Ecosystem management: principles and applications. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Bourgeron, P.S., and M.E. Jensen. 1993. An overview of the ecological principles for ecosystem management. pp. 51–63. In: M.E. Jensen, and P.S. Bourgeron (eds.), Eastside Forest Ecosystem Health Assessment. Volume II. Ecosystem management: principles and applications. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

Braun, E.L. 1950. *Deciduous Forests of Eastern North America.* Blakiston Press, Philadelphia, PA.

Braun-Blanquet, J. 1928. *Pflanzensoziologie. Grundzuge der vegetationskunde.* Springer, Berlin, Germany. [English translation published in 1932 by McGraw-Hill, New York, NY.]

Briggs, J.C. 1974. *Marine Zoogeography.* McGraw-Hill, New York, NY.

Bright, R.C. 1968. Surface-water chemistry of some Minnesota lakes, with preliminary notes on diatoms. Interim Report 3, Limnological Research Center and Bell Museum of Natural History, University of Minnesota, Minneapolis, MN.

Brown, D.E., C.H. Lowe, and C.P. Pase. 1979. A digitized systematic classification system for the biotic communities of North America, with community (series) and association examples for the Southwest. *Journal of the Arizona-Nevada Academy of Science 14* (suppl. 1): 1–16.

Brown, D.E., C.H. Lowe, and C.P. Pase. 1980. A digitized systematic classification for ecosystems with an illustrated summary of the natural vegetation of North America. USDA Forest Service General Technical Report RM-73, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Brown, J.H. 1984. On the relation between the abundance and distribution of species. *American Naturalist* 124: 255–279.

Brown, J.H., and A.C. Gibson. 1983. *Biogeography.* C.V. Mosby, St. Louis, MO.

Bulger, A.J., B.P. Hayden, M.E. Monaco, D.M. Nelson, and M.G. McCormick-Ray. 1993. Biologically-based estuarine salinity zones derived from a multivariate analysis. *Estuaries* 16: 311–322.

Burger, D. 1976. The concept of ecosystem regions in forest site classification. pp. 213–218. In: *Proceedings XVI IUFRO World Congress, Division I, June 20–July 2, 1976, Oslo, Norway.*

Busch, W.-D.N., and P.G. Sly, editors. 1992. *The Development of an Aquatic Habitat Classification System for Lakes.* CRC Press, Boca Raton, FL.

Cajender, A.K. 1926. The theory of forest types. *Acta Forestalia Fennica* 29: 1–108.

Carpenter, K.E. 1928. *Life in Inland Waters.* Macmillan, New York, NY.

Christensen, N.L., A.M. Bartuska, J.H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J.F. Franklin, J.A. MacMahon, R.F. Noss, D.J. Parsons, C. H. Peterson, M.G. Turner, and R.G. Woodmansee. 1996. The report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. *Ecological Applications* 6: 665–691.

Cleland, D.T. 1996. Multifactor classification of ecological land units in northeastern Lower Michigan. Unpublished Ph.D. dissertation. Michigan State University, East Lansing, MI.

Cleland, D.T., J.B. Hart, G.E. Host, K.S. Pregitzer, and C.W. Ramm. 1993. *Ecological classification system for the Huron-Manistee National Forest: field guide.* Huron-Manistee National Forest, Cadillac, MI.

Cleland, D.T., J.B. Hart, G.E. Host, K.S. Pregitzer, and C.W. Ramm. 1994. *Ecological classification and inventory system of the Huron-Manistee National Forest.* USDA Forest Service, Region 9, Milwaukee, WI.

Clements, F.E. 1916. *Plant succession: an analysis of the development of vegetation*. Carnegie Institute of Washington Publication, Washington, D.C.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.

Constanza, R., L. Weinger, C. Faulk and K. Maler. 1993. Modelling complex ecological economic systems. *Bioscience* 43: 545–555.

Cook, J.E. 1995. Implications of modern successional theory for habitat typing: a review. *Forest Science* 42: 67–75.

Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe. 1979. *Classification of the wetlands and deepwater habitats of the United States*. U.S. Fish and Wildlife Service, Washington, D.C.

Crispin, S. 1990. A biological database for monitoring the Great Lakes ecosystem. pp. 43–48. In: J. Kusler, and R. Smardon (eds.), *Proceedings of an International Symposium on Wetlands of the Great Lakes: Protection and Restoration Policies*. May 16–18, 1990, Niagra Falls, New York. Association of State Wetland Managers, Berne, NY.

Curtis, J.T. 1959. *The vegetation of Wisconsin: an ordination of plant communities*. University of Wisconsin Press, Madison, WI.

Daubenmire, R.F. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. *Ecological Monographs* 22: 301–330.

Daubenmire, R.F. 1968. *Plant Communities: A Textbook of Synecology*. Harper Rowe, New York, NY.

Davis, F.W. 1995. Information systems for conservation research, policy and planning: better access to data for scientists, policy makers, and managers. *Bioscience* (suppl.) S36–S42.

Davis, F.W., D.A. Quattrochi, and M.K. Ridd. 1991. Environmental analysis using integrated GIS and remote sensed data: some research needs and priorities. *Photogrammetric Engineering and Remote Sensing* 57: 689–697.

Davis, W.M. 1890. The rivers of northern New Jersey, with note on the classification of rivers in general. *National Geographic Magazine* 2: 82–110.

Denton, D.R. and B.V. Barnes. 1988. An ecological climatic classification of Michigan: a quantitative approach. *Forest Science* 34: 119–138.

DeVelice, R.L., G.J. Daumiller, P.S. Bourgeron, and J.O. Jarvie. 1993. Bioenvironmental representativeness of nature preserves: assessment using a combination of a GIS and a rule-based model. pp. 51–58. In: *Proceedings, First Biennial Scientific Conference on the Greater Yellowstone Ecosystem*, September 1992, National Park Service, Mammoth, WY.

di Castri, F., and A.J. Hansen. 1992. The environment and development crises as determinants of landscape dynamics. pp. 3–18. In: A.J. Hansen, and F. di Castri (eds.), Landscape boundaries: consequences for biotic diversity and ecological flows. Springer-Verlag, New York, NY.

di Castri, F., A.J. Hansen, and M.N. Holland, editors. 1988. A new look at ecotones: emerging international projects on landscape boundaries. *Biology International* Special Issue 17, IUBS, Paris, France.

Dinerstein, E., D.M. Olson, D.J. Graham, A.L. Webster, S.A. Pimm, M.P. Bookbinder, and G. Ledec. 1995. *A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean*. The World Wildlife Fund and The World Bank, Washington, D.C.

Driscoll, R.S., D.L. Merkel, D.L. Radloff, D.E. Snyder, and J.S. Hagihara. 1984. *An ecological land classification framework for the United States*. USDA Forest Service, Miscellaneous Publication 1439, Washington, D.C.

Dunbar, M.J. 1979. The relation between oceans. pp. 112–125. In: S. Van der Spoel, and A.C. Pierrot-Bults (eds.), *Zoogeography and Diversity in Plankton*. Halstead (Wiley), New York, NY.

Ebert, D.J., T.A. Nelson, and J.L. Kershner. 1991. A soil-based assessment of stream fish habitats in Coastal Plain streams. *Proceedings of Warmwater Fisheries Symposium*, June 4–8, 1991, Phoenix, Arizona, USA.

Environment Canada. 1989. *Ecoclimatic regions of Canada, first approximation (with map at a scale of 1: 7,500,000)*. Ecological Land Classification Series No. 23, Environment Canada, Ottawa, Canada.

Ekman, S. 1953. Zoogeography of the sea. Sidgwick and Jackson Ltd., London, UK.

Eyre, F.H. (ed.). 1980. *Forest Cover Types of the United States and Canada*. Society of American Foresters, Washington, D.C.

Fausch, K.D., C.L. Hawkes, and M.G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–1985. USDA Forest Service General Technical Report PNW-GTR-213, Pacific Northwest Research Station, Corvallis, OR.

Fenneman, N.M. 1928. Physiographic divisions of the United States. *Annals Association American Geographers* 18: 261–353.

Fenneman, N.M. 1946. *Physical divisions of the United States (map, scale 1: 7,000,000)*. U.S. Geological Survey, Reston, VA.

Flahault, C., and C. Schroter. 1910. Rapport sur la nomenclature phytogeographique. *Proceedings of the 3rd International Botanical Congress, Brussels* 1: 131–164.

Forman, R.T.T., and M. Godron. 1986. *Landscape Ecology*. Wiley and Sons, New York, NY.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecological Applications* 3: 202–205.

Frayer, W.E., L.S. Davis, and P.G. Risser. 1978. Uses of land classification. *Journal of Forestry* 76: 647–649.

Frissell, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream classification: viewing streams in a watershed context. *Environmental Management* 10: 199–214.

Gallant, A.L., T.R. Whittier, D.P. Larsen, J.M. Omernik, and R.M. Hughes. 1989. Regionalization as a tool for managing environmental resources. EPA/600/3-89/060, U.S. Environmental Protection Agency, Corvallis, OR.

Gauch, H.G., Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, New York, NY.

Gleason, H.A. 1917. The structure and development of the plant association. *Bulletin of the Torrey Botanical Club* 44: 463–481.

Gleason, H.A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7–26.

Greenacre, M.J. 1984. *Theory and Applications of Correspondence Analysis*. Academic Press, London.

Greeson, P.E., J.R. Clark, and J.E. Clark, editors. 1979. Wetland functions and values: the state of understanding. Proceedings National Wetlands Symposium. American Water Resource Association, Technical Publication No. TPS79-2, Minneapolis, MN.

Grossman, D.H., D. Faber-Langendoen, A.S. Weakley, M. Anderson, P. Bourgeron, R. Crawford, K. Goodin, S. Landaal, K. Metzler, K.D. Patterson, M. Pyne, M. Reid, and L. Sneddon. 1998. International classification of ecological communities: Terrestrial vegetation of the United States. Volume I. The national vegetation classification standard. The Nature Conservancy, Arlington, VA.

Grossman, D.H., K.L. Goodin, X. Li, D. Faber-Langendoen, and M. Anderson. 1994a. Standardized national vegetation classification system. Prepared for the USDI National Biological Survey/National Park Service Vegetation Mapping Program, Denver, CO.

Grossman,, D.H., K.L. Goodin, and C.L. Reuss (eds.). 1994b. *Rare plant communities of the conterminous United States: an initial survey*. The Nature Conservancy, Arlington, VA.

Grumbine, R.E. 1994. What is ecosystem management? *Conservation Biology* 8: 27–28.

Hammond, E.H. 1964. Classes of land-surface form in the forty-eight states, U.S.A. (map, scale 1: 5,000,000). *Annals Association American Geographers* 54: Map Supp. No. 4.

Hansen, A.J., and F. di Castri (eds.), 1992. *Landscape Boundaries: Consequences for Biotic Diversity and Ecologic Flows*. Springer-Verlag, New York, NY.

Haufler, J.B. 1994. An ecological framework for planning for forest health. *Journal of Sustainable Forestry* 2: 307–316.

Hawkes, C.L., D.L. Miller, and W.G. Layher. 1986. Fish ecoregions of Kansas: stream fish assemblage patterns and associated environmental correlates. *Environmental Biology of Fishes* 17: 267–279.

Hayden, B.P., and R. Dolan. 1976. Coastal marine fauna and marine climates of the Americas. *Journal of Biogeography* 3: 71–81.

Hayden, B.P., R.D. Dueser, J.T. Callahan, and H.H. Shugart. 1991. Long-term research at the Virginia Coast Reserve. *BioScience* 41: 310–318.

Hayden, B.P., G.C. Ray, and R. Dolan. 1984. Classification of coastal and marine environments. *Environmental Conservation* 11: 199–207.

Hedgpeth, J.W. 1957. Marine biogeography. *Geological Society America Memoir* 67(1): 359–382.

Hengeveld, R. 1990. *Dynamic Biogeography*. Cambridge University Press, Cambridge, UK.

Herbertson, A.J. 1905. The major natural regions: an essay in systematic geography. *Geography Journal* 25: 300–312.

Herdendorf, C.E., C.N. Raphael, and E. Jaworski. 1986. The ecology of the Lake St. Clair wetlands: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.7).

Higgins, J., M. Lammert, D. Grossman, and M. Bryer. 1996. A classification framework for freshwater communities: proceedings of The Nature Conservancy's Aquatic Community Classification Workshop, April 9–11, 1996, New Haven, Missouri. Available from The Nature Conservancy, Arlington, VA.

Hill, M., and W.S. Platts. 1995. *Lower Owens River watershed ecosystem management plan*. Ecosystem Sciences, Boise, ID.

Hill, M.O. 1974. Correspondence analysis: a neglected multivariate method. *Journal Royal Statistical Society, Series C*, 23: 340–354.

Hill, M.O. 1979. Twinspan. A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and the attributes. Cornell University, Ithaca, NY.

Hills, G.A. 1952. The classification and evaluation of sites for forestry. Ontario Department of Lands and Forests, Resource Division Report 24, Toronto, Ontario, Canada.

Hix, D.M. 1988. Multifactor classification of upland hardwood forest ecosystems of the Kickapoo River watershed, southwestern Wisconsin. *Canadian Journal Forest Research* 18: 1405–1415.

Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. *Science* 105: 367–368.

Holdridge, L.R. 1967. *Life Zone Ecology*. Tropical Science Center, San Jose, CA.

Holling, C.S., L. Gunderson, and G. Peterson. 1993. Comparing ecological and social systems. Beijer Discussion Paper, Series #36. Beijer International Institute of Ecological Economics, Royal Swedish Academy of Science, Stockholm, Sweden.

Hooper, F.F. 1969. Eutrophication indices and their relation to other indices of ecosystem change. In: *Eutrophication: Causes, Consequences, Correctives: Proceedings of a Symposium*. National Academy of Sciences, Washington, D.C.

Hornberger, G.M., and E.W. Boyer. 1995. Recent advances in watershed modelling. *Reviews Geophysics* (Suppl. July): 949–957.

Horton, R.E. 1945. Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. *Geological Society of America Bulletin* 56: 275–370.

Host, G.E. 1993. Field sampling and data analysis methods for development of ecological land classifications: an application on the Manistee National Forest. USDA Forest Service General Technical Report NC-162, St. Paul, MN.

Host, G.E., and K.S. Pregitzer. 1991. Ecological species groups for upland forest ecosystems of northern Lower Michigan. *Forest Ecology and Management* 43: 87–102.

Host, G.E., K.S. Pregitzer, C.W. Ramm, J.B. Hart, and D.T. Cleland. 1987. Landform mediated differences in successional pathways among upland forest ecosystems in northwestern Lower Michigan. *Forest Science* 33: 445–447.

Host, G.E., K.S. Pregitzer, C.W. Ramm, D.T. Lusch, and D.T. Cleland. 1988. Variations in overstory biomass among glacial landforms and ecological land units in northwestern Lower Michigan. *Canadian Journal of Forest Research* 18: 659–668.

Howard, J.A., and C.W. Mitchell. 1985. *Phytogeomorphology*. John Wiley and Sons, New York, NY.

Hudson, P.L., R.W. Griffiths, and T.J. Wheaton. 1992. Review of habitat classification schemes appropriate to streams, rivers, and connective channels in the Great Lakes drainage basin. pp. 73–107. In: W.-D.N. Busch, and P.L. Sly (eds.), *The Development of an Aquatic Habitat Classification System for Lakes*. CRC Press, Boca Raton, FL.

Hughes, R.M., S.A. Heiskary, W.J. Matthews, and C.O. Yoder. 1994. Use of ecoregions in biological monitoring. pp. 125–151. In: S.L. Loeb, and A. Spacie (eds.), *Biological Monitoring of Aquatic Systems*. Lewis Publishers, Boca Raton, FL.

Hughes, R.M., E. Rexstad, and C.E. Bond. 1987. The relationship of aquatic ecoregions, river basins, and physiographic provinces to the icthyiographic regions of Oregon. *Copeia* 2: 423–432.

Hutchinson, G.E. 1957. *A Treatise on Limnology*. Vol. 1. Wiley, York, NY.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals. *American Naturalist* 93: 45–159.

IEMTF [Interagency Ecosystem Management Task Force]. 1995. *The ecosystem approach: healthy ecosystems and sustainable economies.* Volumes I–III. U.S. Dept. Commerce, National Technical Information Service, Springfield, VA.

Illies, J. 1961. Versuch einer allgemein biozonotischen Gleiderung der Fliessgewasser. Verhandlungen der Internationalen Verinigung fur theroetische und angewandte. *Limnologie* 13: 834–844.

Jensen, M.E., P.S. Bourgeron, R. Everett, and I. Goodman. 1996. Ecosystem management: a landscape ecology perspective. *Water Resources Bulletin* 32: 1–14.

Johnson, P.S. 1992. Oak overstory/reproduction relations in two xeric ecosystems in Michigan. *Forest Ecology and Management* 48: 233–240.

Jones, R.K., G. Pierpoint, G.M. Wickware, J.K. Jeglum, R.W. Arnup, J.M. Bowles. 1983. *Field guide to forest ecosystem classification for the clay belt, site region 3e.* Ministry of Natural Resources, Toronto, Ontario, Canada.

Kay, J.J. 1991. A nonequilibrium thermodynamics framework for discussing ecosystem integrity. *Environmental Management* 15: 483–495.

Kent, M., and P. Coker. 1992. *Vegetation Description and Analysis.* Belhaven Press, London, UK.

Ketchum, B.K. 1972. *The Waters' Edge: Critical Problems of the Coastal Zone.* Massachusetts Institute of Technology Press, Cambridge, MA.

Keys, J. Jr., C. Carpenter, S. Hooks, F. Koening, W.H. McNab, W. Russell, and M.L. Smith. 1996. Ecological units of the Eastern United States — first approximation. Part I: ARC INFO; Part II: Supporting Imagery; Part III: Text. CD-ROM. USDA Forest Service, Atlanta, GA.

Koestler, A. 1967. *The Ghost in the Machine.* Macmillan, New York, NY.

Komarkova, V. 1983. Comparison of habitat type classification to some other classification methods. pp. 21–31. In: W.H. Moir, and L. Hendzel (eds.), *Proceedings of the Workshop on Southwestern Habitat Types, April 8–10, 1983, Albuquerque, New Mexico.* USDA Forest Service, Southwestern Region, Albuquerque, NM.

Köppen, W. 1931. *Grundriss der Klimakunde.* Walter de Gruyter, Berlin, Germany.

Kotar, J., J.A. Kovach, and C.T. Locey. 1988. *Field guide to forest habitat types of northern Wisconsin.* University of Wisconsin, Department of Forestry and Wisconsin Department of Natural Resources, Madison, WI.

Krajina, V.J. 1965. Biogeoclimatic zones and classification of British Columbia. pp. 1–17. In: Krajina, V.J. (ed.), *Ecology of Western North America.* University of British Columbia, Vancouver, British Columbia, Canada.

Küchler, A.W. 1964. *Potential natural vegetation of the conterminous United States (with separate map at a scale of 1: 3,168,000).* American Geographical Society Special Publication 36, New York, NY.

Küchler, A.W. 1967. *Vegetation Mapping.* Ronald Press, New York, NY.

Küchler, A.W. 1988. Ecological vegetation maps and their interpretation. pp. 469–480. In: A.W. Küchler and I.S. Zonneveld (eds.), *Vegetation Mapping.* Kluwer, Boston, MA.

Küchler, A.W. and I.S. Zonneveld, editors. 1988. *Vegetation Mapping.* Kluwer, Boston, MA.

Larsen, D.P., J.M. Omernik, R.M. Hughes, C.M. Rohm, T.R. Whittier, A.J. Kinney, A.L. Gallant, and D.R. Dudley. 1986. Correspondence between spatial patterns in fish assemblages in Ohio streams and aquatic ecoregions. *Environmental Management* 10: 815–828.

Lawton, J.H., S. Nee, A.J. Letcher, and P.H. Harvey. 1993. Animal distributions: patterns and processes. pp. 41–58. In: P.J. Edwards, R.M. May, and N.R. Webb (eds.), *Large-scale Ecology and Conservation Biology.* Blackwell Scientific, Oxford, UK.

Leach, J.H., and R.C. Herron. 1992. A review of lake habitat classification. pp. 27–57. In: W.-D.N Busch, and P.G. Sly (eds.), *The Development of an Aquatic Habitat Classification System for Lakes.* CRC Press, Boca Raton, FL.

Leopold, L.B., and M.G. Wolman. 1957. River channel patterns: braided, meandering and straight. U.S. Geological Survey Professional Paper 422H, Washington, D.C.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1942–1968.

LOICZ. 1996. Coastal facts. *Land Ocean Interactions Coastal Zone Newsletter* 1: 2.

Lotspeich, F.B. 1980. Watershed as the basic ecosystem: this conceptual framework provides a basis for a natural classification system. *Natural Resources Bulletin* 16: 581–586.

Lotspeich, F.B., and W.S. Platts. 1982. An integrated land-aquatic classification system. *North American Journal of Fisheries Management* 2: 138–149.

Lubchenco, J., A.M. Olson, L.B. Brubaker, S.R. Carpenter, M.M. Holland, S.P. Hubbell, S.A. Levin, J.A. MacMahon, P.A. Matson, J.M. Melillo, H.A. Mooney, C.H. Peterson, H.R. Pulliam, L., S.A. Real, P.J. Regal, and P.G. Risser. 1991. The sustainable biosphere initiative: an ecological research agenda. A Report from the Ecological Society of America. *Ecology* 72: 371–412.

Lyons, J. 1989. Correspondence between the distribution of fish assemblages in Wisconsin streams and Omernik's ecoregions. *American Midland Naturalist* 122: 163–182.

MacKey, B.G., H.A. Nix, M.F. Hutchinson, and J.P. MacMahon. 1988. Assessing representativeness of places for conservation reservation and heritage listing. *Environmental Management* 12: 501–514.

MacKey, B.G., H.A. Nix, J.A. Stein and S.E. Cork. 1989. Assessing the representativeness of the wet tropics of Queensland World Heritage property. *Biological Conservation* 50: 279–303.

Maltby, L.S., G.B. McCullough, and E.Z. Bottomley. 1983. *Baseline studies of 35 selected southern Ontario wetlands.* Canadian Wildlife Service, Ottawa, Canada.

Maxwell, J.R., C.J. Edwards, M.E. Jensen, S.J. Paustian, H. Parrott, and D.M. Hill. 1995. A hierarchical framework of aquatic ecological units in North America. USDA Forest Service General Technical Report NC-176, North Central Forest Experiment Station, St. Paul, MN.

McGowan, J.A. 1971. Oceanographic biogeography of the Pacific. pp. 3–74. In: B.M. Funnell, and W.R. Riedel (eds.), *The Micropaleontology of Oceans.* Cambridge University Press, Cambridge, UK.

McGowan, J.A. 1972. The nature of oceanic ecosystems. pp. 9–28. In: C.B. Miller (ed.), *The Biology of the Oceanic Pacific.* Oregon State University Press, Corvallis, OR.

McNab, W.H., and P.E. Avers, editors. 1994. *Ecological subregions of the United States: section descriptions.* USDA Forest

Service Administrative Publication WO-WSA-5, Washington, D.C.

Meador, M.R., C.R. Hupp, T.F. Cuffney, and M.E. Gurtz. 1993. Methods for characterizing stream habitat as part of the National Water-Quality Assessment Program. U.S. Geological Survey Open File Report 93–408, Reston, VA.

Merriam, C.H. 1898. Life zones and crop zones of the United States. U.S. Department of Agriculture Division Biological Survey, Bulletin 10, Washington, D.C.

Mitsch, W.J., and J.G. Gosselink. 1986. *Wetlands.* Van Nostrand Reinhold, New York, NY.

Monsi, M. 1960. Dry matter reproduction in plants. I. Schemata of dry matter reproduction. *Botanical Magazine* 73: 81–90.

Morrison, D.F. 1976. *Multivariate Statistical Methods.* McGraw-Hill, New York, NY.

Moyle, J.B. 1956. Relationships between chemistry of Minnesota surface waters and wildlife management. *Journal of Wildlife Management* 20: 303–320.

Mueller-Dombois, D. and H. Ellenberg. 1974. *Aims and Methods of Vegetation Ecology.* Wiley, New York, NY.

Muller, P. 1974. *Aspects of Zoogeography.* W. Junk, The Hague, Netherlands.

Naeem, S., L.J. Thompson, S.P. Lawler, J.H. Lawton, and R.M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734–737.

Naiman, R.J., D.G. Lonzarich, T.J. Beechie, and S.C. Ralph. 1992. General principles of classification and the assessment of conservation potential in rivers. In: P.J. Boon, P. Calow, and G.E. Petts (eds.), *River Conservation and Management.* Wiley, Chichester, UK.

Nelson, R.L., W.S. Platts, D.P. Larsen, and S.E. Jensen. 1992. Trout distribution and habitat in relation to geology and geomorphology in the North Fork Humboldt River drainage, northeastern Nevada. *Transactions of the American Fisheries Society* 121: 405–426.

Nix, H.A. 1982. Environmental determinants and evolution in Terra Australia. pp. 47–66. In: W.R. Barker, and P.J.M. Greenslade (eds.), editors. *Evolution of the Flora and Fauna of Arid Australia.* Peacock Publications, Frewville, Australia.

NOAA [National Oceanographic and Atmospheric Administration]. 1985. *National estuarine inventory: data atlas. Volume 1: physical and hydrologic characteristics.* NOAA-NOS Strategic Assessment Branch, Washington, D.C.

Noy-Meir, I. 1973. Data transformations in ecological ordination. I. Some advantages of non-centering. *Ecology* 61: 329–341.

Odum, F.P. 1971. *Fundamentals of Ecology.* Third edition. W.B. Saunders, Philadelphia, PA.

Ogden, J.C., J.W. Porter, N.P. Smith, A.M. Szmant, W.C. Jaap, and D. Forcucci. 1994. A long-term interdisciplinry study of the Florida Keys seascape. *Bulletin of Marine Science* 54: 1059–1071.

Omernik, J.M. 1986. Ecoregions of the conterminous United States (map, scale 1: 7,500,000). U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, OR.

Omernik, J.M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* 77: 118–125.

Omernik, J.M. 1995. Ecoregions: a framework for environmental management. pp. 49–62. In: W. Davis, and T. Simon (eds.), *Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making.* Lewis Publishers, Boca Raton, FL.

Omernik, J.M., and A.L. Gallant. 1987. Ecoregions of the southwest states (map, scale 1: 2,500,000). EPA/600/D-87/316, U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, OR.

Omernik, J.M., and A.L. Gallant. 1989. Defining regions for evaluating environmental resources. Unpublished manuscript prepared for Global Natural Resource Monitoring and Assessment, Preparing for the 21st Century, September 24–30, 1989, Venice, Italy. Available from U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, OR.

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, NJ.

Orians, G.H. 1975. Diversity, stability and maturity in natural systems. pp. 139–150. In: W.H. van Dobben and R.H. Lowe-McConnell (eds.), *Unifying Concepts in Ecology.* W. Junk, The Hague, Netherlands.

Paulsen, S.G. and R.A. Linthurst. 1994. Biological monitoring in the Environmental Monitoring and Assessment Program. In: A.L. Loeb, and A. Spacie (eds.), *Biological Monitoring of Aquatic Systems.* Lewis Publishers, Boca Raton, FL.

Peet, R.K. 1980. Ordination as a tool for analyzing complex data sets. *Vegetatio* 42: 171–174.

Peters, R.H. 1976. Tautology in evolution and ecology. *American Naturalist* 110: 1–12.

Pfister, R.D., and S.F. Arno. 1980. Classifying forest habitat types based on potential climax vegetation. *Forest Science* 26: 52–70.

Pfister, R.D., B.L. Kovalchik, S.F. Arno, and R.C. Presby. 1977. Forest habitat types of Montana. USDA Forest Service General Technical Report INT-34, Intermountain Forest and Range Experiment Station, Ogden, UT.

Pielou, E.C. 1977. *Mathematical Ecology.* Wiley, New York, NY.

Pielou, E.C. 1979. *Biogeography.* Wiley-Interscience, New York, NY.

Pinay, G., A. Fabre, P.H. Vervier and F. Gazelle. 1992. Control of C, N, P distribution in soils of riparian forest. *Landscape Ecology* 6: 121–132.

Platts, W.S. 1979. Including the fishery system in land planning. USDA Forest Service. General Technical Report INT-60, Intermountain Forest and Range Experiment Station, Ogden, UT.

Platts, W.S. 1980. A plea for fishery habitat classification. *Fisheries* 5(1): 2–6.

Pojar, J., K. Klink, and J. Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. *Forest Ecology and Management* 22: 119–154.

Pregitzer, K.S., and B.V. Barnes. 1982. The use of ground flora to indicate edaphic factors in upland ecosystems of the McCormick Experimental Forest, Upper Michigan. *Canadian Journal of Forest Research* 12: 661–672.

Prentice, I.C. 1977. Non-metric ordination methods in ecology. *Ecology* 65: 85–94.

Pritchard, D.W. 1967. What is an estuary? pp. 3–5. In: G.H. Lauff (ed.), *Estuaries.* AAAS Press, Washington, D.C.

Raunkier, C. 1937. *Plant Life Forms.* Clarendon Press, Oxford, UK.

Ray, G.C. 1991. Coastal-zone biodiversity patterns. *BioScience* 41: 490–498.

Ray, G.C., and B.P. Hayden. 1992. Coastal zone ecotones. pp. 403–420. In: F. di Castri, and A.J. Hansen (eds.), *Landscape Boundaries: Consequences for Biodiversity and Ecological Flows*. Springer-Verlag, New York, NY.

Ray, G.C., B.P. Hayden, M.G. McCormick-Ray, and T.M. Smith. 1997. Land-seascape diversity of the U.S. East Coast coastal zone with particular reference to estuaries. pp. 357–371. In: R.F.G. Ormond, J. Gage, and M.V. Angel (eds.), *Marine Biodiversity: Causes and Consequences*. Cambridge University Press, Cambridge, UK.

Reid, M.S., P.S. Bourgeron, H.C. Humphries, and M.E. Jensen. 1995. Documentation of the modeling of potential vegetation at three spatial scales using biophysical settings in the Columbia River Basin Assessment Area. Unpublished report prepared for the USDA Forest Service, contract # 53-04H1-6890, by the Western Heritage Task Force, The Nature Conservancy, Boulder, CO.

Reppert, R.T., and W. Sigleo. 1979. *Wetland values: concepts and methods for wetland evaluation*. U.S. Army Institute for Water Resources, Fort Belvoir, VA.

Rhom, C.M., J.W. Giese, and C.C. Bennett. 1987. Evaluation of an aquatic ecoregion classification of streams in Arkansas. *Journal Freshwater Ecology* 4: 127–140.

Ricker, W.E. 1934. An ecological classification of certain Ontario streams. *Publication of the Academy of Natural Sciences of Philadelphia* 101: 277–341.

Robins, C.R. 1971. Distributional patterns of fishes from coastal and shelf waters of the tropical western Atlantic. pp. 249–255. In: *Symposium on Investigations and Resources of the Caribbean Sea and Adjacent Regions*. FAO Papers on Fisheries Resources, FAO, Rome, Italy.

Robins, C.R. 1992. *Saltwater Fish*. Smithmark, New York, NY.

Robins, C.R., and G.C. Ray. 1986. *A Field Guide to Atlantic Coast Fishes of North America*. Houghton Mifflin, Boston, MA.

Rolof, G.J. 1994. Using an ecological classification system and wildlife habitat models in forest planning. Ph.D. dissertation, Michigan State University, East Lansing, MI.

Rowe, J.S. 1961. The level-of-integration concept and ecology. *Ecology* 42: 420–427.

Rowe, J.S. 1972. *Forest regions of Canada (with separate map at a scale of 1: 6,336,000)*. Publication No. 1300, Canadian Forestry Service, Ottawa, Ontario, Canada.

Rowe, J.S. 1980. The common denominator in land classification in Canada: An ecological approach to mapping. *Forestry Chronicle* 6: 19–20.

Rowe, J.S. 1984. Forestland classification: limitations of the use of vegetation. pp. 132–147. In: J.G. Bockheim (ed.), *Forest Land Classification: Experiences, Problems, Perspectives*. Proceedings of the symposium, March 18–20, 1984. University of Wisconsin, Madison, WI.

Rowe, J.S., and J.W. Sheard. 1981. Ecological land classification: a survey approach. *Environmental Management* 5: 451–464.

Roy, P.S. 1984. New South Wales estuaries: their origin and evolution. pp. 99–121. In: B.G. Thom (ed.), Coastal geomorphology in Australia. Academic Press, Sydney, Australia.

Rübel, E. 1930. *Die pflanzengesellschaften der Erde*. Huber Verlag, Bern, Switzerland.

Schupp, D.H. 1992. An ecological classification of Minnesota lakes with associated fish communities. Minnesota Department of Natural Resources Investigation Report 417, Minneapolis, MI.

Scott, J.M., F. Davis, B. Csuti, R. Noss, B. Buttterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T.C. Edwards, Jr., J. Ullman, and R.G. Wright. 1993. Gap analysis: protecting biodiversity using geographic information systems. *Wildlife Monographs*, 123.

Seaber, P.R., F.P. Kapinos, and G.L. Knapp. 1984. State hydrologic unit maps. U.S. Geological Survey Open-file Report 84-708, U.S. Geological Survey, Reston, VA.

Shannon, E.E., and P.L. Brezonik. 1972. Eutrophication analysis: a multivariate approach. *Journal of the Sanitary Engineering Division of the American Society of Civil Engineers* 98 (SA1): 37–57.

Sheldon, A.L. 1972. A quantitative approach to the classification of inland waters. pp. 205–261. In: J.V. Krutilla (ed.), *Natural environments: studies in theoretical applied analysis*. Johns Hopkins Press, Baltimore, MD.

Shelford, V.E. 1911. Ecological succession. I. Stream fishes and method of physiographic analysis. *Biological Bulletin* 21: 9–35.

Shimwell, D.W. 1971. *The Description and Classification of Vegetation*. University of Washington Press. Seattle, WA.

Sims, R.A., W.D. Towill, K.A. Baldwin, and G.M. Wickware. 1989. *Field guide to the forest ecosystem classification for northwestern Ontario*. Forestry Canada, Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada.

Sly, P.G., and W.-D.N. Busch. 1992. A system for aquatic habitat classification of lakes. pp. 15–26. In: W.-D.N. Busch, and P.G. Sly (eds.), *The Development of an Aquatic Habitat Classification System for Lakes*. CRC Press, Boca Raton, FL.

Spies, T.A., and B.V. Barnes. 1985. A multifactor ecological classification of the northern hardwood and conifer ecosystems of Sylvania Recreation Area, Upper Peninsula, Michigan. *Canadian Journal of Forest Research* 15: 949–960.

Stearns, S.C. 1976. Life history tactics: a review of the ideas. *Quarterly Review of Biology* 51: 3–47.

Steele, J.H. 1989. The ocean "landscape." *Landscape Ecology* 3: 186–192.

Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. *American Geophysical Union Transactions* 38: 913–920.

Strong, W.L., E.T. Oswald, and D.J. Downing. 1990. The Canadian vegetation classification system, first approximation. National Vegetation Working Group, Canadian Committee on Ecological Land Classification. Ecological Land Classification Series, No. 25, Sustainable Development, Corporate Policy Group, Environment Canada, Ottawa, Ontario, Canada.

Sukachev, V. 1945. Biogeocoenology and phytocoenology. *C.R. Academy of Science, USSR*. 47: 429–431.

Swanson, F.J., T.K. Kratz, N. Caine, and R.G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. *Bioscience* 38: 92–98.

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

Tiner, R.W., Jr. 1984. *Wetlands of the United States: current status and recent trends*. U.S. Fish and Wildlife Service, U.S. Government Printing Office, Washington, D.C.

Tonn, W.M. 1990. Climate change and fish communities: a conceptual framework. *Transactions of the American Fisheries Society* 119: 337–352.

Tonn, W.M., and J.J. Magnuson. 1982. Patterns in species composition and richness in fish assemblages in northern Wisconsin lakes. *Ecology* 63: 1149–1166.

Trewartha, G.T. 1968. *Introduction to Climate.* 4th edition. McGraw-Hill, New York, NY.

Troll, C. 1941. Studien zur vergleichenden Geographie der Hochgebirge. Bonn: Friedrich Wilhelm Universitat, Bericht 23: 94–96.

Troll, C. 1943. Die Frostwechselhaufigkeit in den Luft - und Bodenklimaten der Erde. *Meteororologische Zeitschrift* 60: 161–171.

Troll, C. 1955. Der jahreszeitliche Ablauf des Naturgeschehens in den verschiedenen Klimagurteln der Erde. *Studium Generale* 8: 713–733.

Troll, C. 1956. *Der Klima- und Vegetationsaufbau der Erde im Lichte neuer Forschungen.* Akademie der Wissencschaften und Literatur, Mainz, pp. 216–229.

Tüxen, R. 1956. Die heutige potentielle natürliche vegetation als Gegenstand der Vegetationskartierung. *Angew. Pflanzensoziol. (Stolzenau, Weser)* 13: 5–42.

Udvardy, M.D.F. 1975. A classification of the biogeographical provinces of the world. International Union for Conservation of Nature and Natural Resources, Occasional Paper No. 18. Morges, Switzerland

UNESCO [United Nations Educational, Scientific and Cultural Organization]. 1973. International Classification and Mapping of Vegetation, Series 6, Ecology and Conservation. UNESCO, Paris, France.

Urban, D.L., R.V. O'Neill, and H.H. Shugart, Jr. 1987. Landscape ecology: a hierarchical perspective can help scientists understand spatial patterns. *Bioscience* 37: 119–127.

USDA Soil Conservation Service. 1981. *Land resource regions and major land resource areas of the United States.* Agriculture Handbook No. 296, USDA Soil Conservation Service, Washington, D.C.

USGS [United States Geological Survey]. 1982. *Hydrologic unit map of the United States.* U.S. Government Printing Office, Washington, D.C.

Valiela, I. 1984. *Marine Ecological Processes.* Springer-Verlag, New York, NY.

Walter, H. 1973. *Die vegetation der Erde I. Tropische and subtropische Zonen.* Third edition. Fisher, Jena, Stuttgart, Germany.

Walter, H. 1985. *Vegetation of the earth, and ecological systems of the geobiosphere.* Third edition. Springer-Verlag, New York, NY.

Walter, H., and E. Box. 1976. Global classification of natural terrestrial ecosystems. *Vegetatio* 32: 75–81.

Warren, C.E. 1979. Toward classification and rationale for watershed management and stream protection. Report No. EPA-600/3-79-059, United States Environmental Protection Agency, Corvalis, OR.

Webb, L.J., J.G. Tracey, W.T. Williams, and G.N. Lance. 1970. Studies in the numerical analysis of complex rainforest communities. V. A comparison of the properties of floristic and physiognomic-structural data. *Journal of Ecology* 58: 203–232.

Wergner, M.J.A. and J.T.C. Sprangers. 1982. Comparison of floristic and structural classification of vegetation. *Vegetatio* 50: 175–183.

Wertz, W.A., and J.A. Arnold. 1972. *Land Systems Inventory.* USDA Forest Service, Intermountain Region, Ogden, UT.

esthoff, V., and A.J. den Held. 1969. *Plantengemenschappen in Nederland.* Thieme, Zutphen.

Westhoff, V., and E. van der Maarel. 1978. The Braun–Blanquet approach. Chapter 20. In: R.H. Whittaker (ed.), *Classification of Plant Communities.* W. Junk, The Hague, Netherlands.

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Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26: 1–80.

Whittaker, R.H. 1962. Classification of natural communities. *Botanical Review* 28: 1–239.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213–351.

Whittaker, R.H. 1975. *Communities and Ecosystems.* Second edition. MacMillan, New York, NY.

Whittaker, R.H. (ed.). 1978. *Classification of Plant Communities.* W. Junk, The Hague, Netherlands.

Whittaker, R.H. (ed.), 1980. *Classification of Plant Communities.* Volume II. W. Junk, The Hague, Netherlands.

Whittier, T.R., R.M. Hughes, and D.P. Larsen. 1988. Correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1264–1278.

Wiken, E.B., compiler. 1986. Terrestrial ecozones of Canada. Ecological Land Classification Series No. 19, Environment Canada, Lands Directorate, Ottawa, Ontario, Canada.

Winter, T.C. 1977. Classification of the hydrologic settings of lakes in the north central United States. *Water Resources Research* 13: 753–767

Witmer, R.E. 1978. U.S. Geological Survey land-use and land-cover classification system. *Journal of Forestry* 76: 661–668.

Zak, D.R., G. E. Host, and K.S. Pregitzer. 1989. Regional variability in nitrogen mineralization, nitrification, and overstory biomass in northern Lower Michigan. *Canadian Journal Forest Research* 19: 1521–1526.

Zak, D.R., K.S. Pregitzer, and G.E. Host. 1986. Landscape variation in nitrogen mineralization and nitrification. *Canadian Journal Forest Research* 16: 1258–1263.

Zonneveld, I.S. 1988. Landscape (ecosystem) and vegetation maps, their relation and purpose. pp. 481–486. In: A.W. Küchler, and I.S. Zonneveld (eds.). *Vegetation Mapping.* Kluwer, Boston, Massachusetts.

Zonneveld, I.S. 1989. The land unit — a fundamental concept in landscape ecology, and its application. *Landscape Ecology* 3: 67–86.