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CLASSIFICATION OF NON-MARINE ECOSYSTEMS

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INTRODUCTION TO THE ECOSYSTEM CONCEPT

The concept of vegetation (versus flora) has seemed a fairly clear one for many years, as a term for the plant-cover of the earth, or any part of it (Egler 1942). Flora, often confused with vegetation, is used for any enumeration or account of the species that occur in a given area, region or other spatial unit.

Vegetation is an easy concept to grasp, as it is usually visible, and often characterized by apparently discontinuous variation, making it amenable to classification and mapping. There seems to be no suitable comparable term applying to animals or animal communities. Fauna is a comparable term to flora, an enumeration or account of the animal species in an area, region, or other spatial unit. Fauna is often also used for the zoological equivalent of the botanical concept of vegetation, but the use of the same term for two related concepts is not a satisfactory arrangement. However, a term for this equivalent zoological concept will not be coined here, as such a term should be very carefully chosen and agreed upon by at least a substantial number of zoologists and zoogeographers. Zoocoenosis would be a possibility, but the series of terms including this one, though very logical, has not met with general acceptance outside continental

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Europe. These terms will be discussed later in this paper along with other existing schemes.

von Bertalanffy is generally given credit for founding General Systems Theory (first codified in von Bertalanffy 1951). It was this theory, intended as a unifying concept for all scientific endeavor, along with the organismic theory of vegetation succession and climax (Clements 1928, 1936), that inspired Tansley to coin the term "ecosystem" in 1935 for a community of organisms interacting with their physical and biotic environment. There has always been a need for a more general term, inclusive of vegetation, its zoological equivalent, and the environment. Tansley's new term satisfied this need very well. He subsequently seldom used the term or concept, and it was not generally adopted for many years. Egler, in the 1940's or early 1950's, used it informally in correspondence. Francis Evans (1956), formally adopted and clearly defined it. It was then used, at least casually, by several American and Australian ecologists. In 1960, at the 10th Pacific Science Congress, Fosberg used and discussed the term "ecosystem" in a major symposium entitled "Man's Place in the Island Ecosystem" (Fosberg 1963). He also used it in a paper entitled "A Qualitative Description of the Coral Atoll Ecosystem" (Fosberg 1961b), which did not receive wide notice. In the introduction to the 1960 symposium, Fosberg discussed the concept in the sense that we will use it in the present paper. For a more complete history, see Major (1969).

Sukachev's Terminology: Over several decades, Professor V. N. Sukachev [W. N. Sukatschew] developed a system for classifying Russian ecosystems incorporating both organisms and environment (Sukachev 1945). His system of terminology, or parts of it, has appeared in various Central European works, but it has never been accepted by Anglo-American writers. His terms "biocoenosis," "phytocoenosis," "zoocoenosis," "biogeocoenosis," "biogeocoenology," and their derivatives, with meanings self-evident from their Greek roots, are perhaps the clearest and least misused terms in ecology. They perhaps could (or should) be substituted generally for their confused English equivalents, except that we should retain the easier term "ecosystem" (instead of biogeocoenosis).

Abstract versus Concrete Ecosystems

The ecosystem concept must be understood, in an abstract sense, as any biological community of one or more organisms plus, and interacting with, its environment. In this sense it would apply to any such system, from a single bacterial cell in a minute drop of water, to the earth with all of its organic inhabitants and all environmental entities that affect them. In its concrete sense, ecosystem applies to any particular spatial unit or stand with its included organisms and the environment with which they interact or by which they are affected. The problem of distinguishing between the abstract (type) and the concrete (example) will be with us as we examine every level in the hierarchy of ecosystem classification.

Confusing Ecosystem and Vegetation Classifications

There has been an unbelievable amount of discussion and a plethora of publications on flora, "vegetation," animal communities and ecological concepts, and an attempt to describe and summarize them, if adequate, would require a book, rather than a review paper. By far the greater part of pertinent work on vegetation and ecosystem concepts and classifications has been done in local, or geographically restricted investigations, usually not claimed to be of more than local application. Some authors, however, assume a broader applicability than is warranted, extrapolating from local observations, making generalizations that apply less and less well the farther one goes from the area where the observations were made.

A considerable number of vegetation classifications have been proposed, described and applied, a few on a general or world scale, many more for restricted areas. A dichotomy has developed between those few classifications which are based strictly on plant or vegetational features, and those including in their definitions such environmental features as climate, soils, moisture, or even animals. In this paper, the term "vegetation" will only refer to the plant component of ecosystems being discussed. In this restricted sense, circularity of reasoning can be avoided. Vegetation cannot at the same time be defined by soil features and then be used to define or characterize soils, for example.

Granting this restriction, most so-called vegetation classifications and the maps based on them are really ecosystem classifications and ecosystem maps. Few vegetation students and mappers are willing to accept this restriction, and most continue to call their schemes vegetation systems and maps. The Engler and Drude (1902), Rübel (1930), Braun-Blanquet (1932), and Fosberg (1961a, 1961c, 1967) systems are the principal early schemes to truly or even primarily qualify as vegetation classification systems on a general or world scale.

PROBLEMS OF DEFINITION AND DELIMITATION

Before considering the existing classifications, it seems appropriate to discuss the problems encountered in defining and delimiting ecosystems as they have concrete existence in the field, and determining how, if possible, they may be related in a hierarchical system. One is intuitively aware, once one grasps the ecosystem concept, that ecosystems, in the concrete sense, exist as discrete entities.

It is no accident that there has been a great deal of description and classification of what has been considered as vegetation, i.e., plant cover. Vegetation can be seen and its variations described and measured. The plant component is clearly the most tangible of the complex of features and qualities that make up most terrestrial ecosystems.

Ideally, of course, an ecosystem should be delimited by taking into account all of its components or attributes. But for practical reasons this is generally impossible. In practice, some of the components may be measured or defined in terms of other components. Soil surveying and mapping, after the reality of a soil type is established by actual sampling, are done by observing vegetation correlation with soils, and mapping the vegetation on the assumptions that the limits of the soil type are indicated by the boundaries or areal extent of the corresponding vegetation.

A first approximation of the extent and boundaries of an ecosystem may thus be established by discerning and mapping a vegetation feature or complex of features. This is the property of the ecosystem that is immediately visible and may possibly indicate the extent and boundaries of the ecosystem under study. If adequate spot-checking of other important but less obvious features or properties of the system (e.g., soils) establishes that the spatial extent of the vegetation corresponds with that of the corresponding ecosystem, we have a practical basis for placing it in a classification and determining the set of phenomena that we are interested in.

Inventories of Organisms

In characterizing an ecosystem at any level it would seem necessary to list or inventory two sets of phenomena - the biotic or living component - flora and fauna, and the inorganic environmental features. Neither of these enterprises is easy. On the organic side, such large and conspicuous animals as birds and mammals are fairly easy to identify and count. Likewise trees are large and obvious - witness the frequent inventories of plants (trees) 10 cm or more diameter at breast height. Shrubs, vines, and herbs are fairly easy, but often disregarded. But the cryptic, small or tiny organisms - earthworms, salamanders, insects, spiders, mites, nematodes, fungi, actinomycetes, protozoa, algae, and bacteria - that make up by far the greatest number of species in any natural ecosystem are a different matter altogether. To complete such an inventory requires either an old fashioned across-the-board naturalist or a team of specialists.

Inventories of Inorganic Features

Likewise, the inorganic components of an ecosystem (e.g., the soils, landforms, water) must be identified, measured, their ranges of variation determined, their synergistics and their effects on the living components understood and identified. Again, this is no mean array of tasks, but it is necessary if an ecosystem is to be fully understood as a functioning whole.

Use of Selected Features or Components

Clearly, to inventory and evaluate all organic and inorganic components of ecosystems to be classified would be totally impractical. No classification would ever be accomplished. What, then, is the alternative? It seems clear that a few important and readily observable attributes must be selected and assumed to be the parameters that define the ecosystems at any particular level in the hierarchy. Different such sets of features would be suitable at different levels, and an estimation of the breadth and importance of major features or sets of features would determine the levels and their order in the hierarchy. At least for the higher parts of the hierarchy, the science of biogeography should be enlisted to help select these criteria. To the best of our knowledge, this approach has not been tried, although some of the so-called vegetation classifications, those in which broad environmental, rather than strictly vegetation characteristics, are basic, may actually be the results of similar logic.

Biogeography

Biogeography may be thought to provide an approach to an ecosystem classification but there is so much difference of opinion as to what is biogeography that this confusion must be put in order before it will be very useful for anything of this sort. There seem to be at least four main subject-matters referred to as biogeography or its two subdivisions phytogeography and zoogeography (Fosberg 1976):

1. Floristic/faunistic biogeography, perhaps better called statistical biogeography, is perhaps what is most commonly meant by the term. In this, plant and animal species are sorted into groups called "elements" based on what are considered to be their closest taxonomic relationships. Then these groups are arranged geographically into "geographic elements." A preponderance of any one of these in a flora or fauna indicates its principal geographic affinity. This seems theoretically a sound approach, and is applied in many biogeographic studies and texts. However, the uneven and frequently inadequate taxonomic knowledge in many major groups of organisms and incompleteness of collection in many geographic areas lessens one's confidence in conclusions reached in this way.

2. Another major field of biogeography is called historical biogeography. This attempts to interpret and understand distributional patterns in terms of what is known of the fossil histories of faunas and floras, and of paleogeographic reconstructions. These approaches not only contribute to the development of a biogeographic picture of the biota of an area or region, but what is known of the biota helps fill in the paleogeography and the knowledge of the migration and evolution of the plant and animal groups and lines of descent (e.g., vicariance *versus* dispersal theories of biogeography (Udvardy 1981) or the "equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967)).

The results of these sorts of biohistorical speculations, correlations, and reconstructions are often combined with determination of the succession of strata. The apparent chronology provides materials for stratigraphic determination of the relative ages of strata and their included fossils. Then the presence of taxonomically similar fossils may be used to indicate the age of other strata in which these fossils occur. The lists of fossils of putatively similar ages are compiled into fossil floras and faunas. These may then be assumed to indicate paleo-ecosystems. However, there seems to be so much incompleteness and inherent uncertainty in the results of this approach that historical biogeography can scarcely contribute much to a practical ecosystem classification.

3. Economic biogeography is the collection and organization of information on useful plants and animals, and products derived from them in terms of their geographic origins and distributions. This is a special aspect of biogeography of considerable practical importance, but it has little pertinence to ecosystem definition and classification.

4. There remains the subject of ecological or physiological biogeography. This, the classical, or Schimperian biogeography, usually phytogeography, had its origin in Humboldt's observation of zonal distribution of organisms according to attitudinal belts in the Ecuadorian Andes (Humboldt 1805, 1806). It was launched as a formal science by A.F.W. Schimper in 1898, in his monumental "Pflanzengeographie Auf Physiologischer Grundlage" (first translated into English in 1903 by W. R. Fisher). This great work divides the land surfaces of the earth into plant-geographic regions on the basis of climate, temperature and rainfall regimes, soils, elevation, and other ecological factors, as expressed by the structure and physiognomy of the vegetation. On a world scale, this scheme resulted in a very coarse-grained pattern, but an eminently sound one. It is, of course, really an arrangement of major ecosystems, though commonly referred to as a vegetation system. Much work has been devoted to refinement and improvement of Schimper's essentially physiognomically definable and recognizable units. It has been given more attention by geographers than botanists or zoologists, but it is basically ecological. Schimper's regions and subdivisions are in reality major ecosystems based on complexes of ecological factors and recognizable from variations in physiognomy of vegetation. Modern refinements of these units will most likely form the higher levels of any hierarchical classification of ecosystems. As noted earlier in this paper, vegetation is the most visible feature of almost any major ecosystem and its nature and appearance provide the best indicators of the ecosystem extent and boundaries.

Aquatic Situations

Aquatic ecosystems do not fit well with much of what has been said above, which is mostly about dry-land or wet-land terrestrial phenomena. Large bodies of water, marine benthos, small lakes and ponds, streams and rivers, and flowing springs cannot ordinarily be identified and defined by readily visible vegetation. They certainly contain biotic communities in addition to their physical environments, but their environments provide water rather than soil and air as the medium or matrix. In some cases the vegetation is evident enough to be useful in defining the system, but in others we must depend on other features such as chemical or physical structure of the water medium. The water may be saline or fresh, acid or alkaline, clear or turbid, still or moving, smooth or turbulent, warm or cold, seasonally frozen or not, and more or less (usually more, these days) polluted. These features and combinations of them will influence or control the organic components of the system. An almost infinite number of combinations may occur. It seems clear that the whole natural range of ecosystems should be divided into terrestrial and aquatic segments, each of which would comprise a separate hierarchy in any complete hierarchical classification. It will be difficult to determine which of the sets of features listed above under the aquatic environment are useful to our purposes. Those pairs of attributes are not the only ones of significance, but seem to be the most important in order to provide bases for a usable hierarchy.

Succession and Continuous Variation

The problem of succession will have to be dealt with in both aquatic and terrestrial ecosystems. Clements (1902, 1928) has provided a rather clear framework in his hydrosere-halosere-xerosere terminology. His hydrosere is perhaps the easiest to visualize, though all too easy to oversimplify. Emergent aquatic vegetation, especially on tidally or other intermittently submerged and emerged ground (and continua), whether successional, non-successional, geographic or periodic, are realities to be dealt with. This is most especially true when our most basic discontinuity, that between aquatic and terrestrial ecosystems, breaks down. The truism that sharp boundaries are rare or non-existent in nature is nowhere more evident than here. Even the apparently sharpest boundaries are made fuzzy by "edge effects."

Diversity

A concept that has, to a few scientists, been of importance for a long time, has in the last few years been recognized to be of major consequence to a wide audience. Diversity has come to be recognized as a factor in the stability and permanence of major ecosystems. Such a subject, attracting more than just scientific attention, and now even of political consequence, is certain to stir up controversy. Even the definition of diversity, once regarded as obvious, has become a matter of argument with some definitions so mathematical as not to be obvious at all.

A stated objective of many classifications is the preservation and protection of biological diversity. Diversity must therefore enter into the classification of ecosystems. What most organizations intend to preserve is actual diversity in terms of numbers of species. These are essential components of functioning ecosystems, clear and simple enough to be readily understood by educated and intelligent people, and not only by specialists in technical ecology.

While the objective is the preservation of the mosaic of complex communities of interacting organisms, the habitats that are home to the diverse multitudes of species are equally diverse. The geological base may be of many kinds, physical and chemical, of rocks, the parent materials for a diversity of soils. Erosion and tectonic uplift of these, and volcanic outpouring from the complex series of magmas forming and combining beneath the surface of the earth, and the erosion and weathering of surface rocks provide a rich diversity of habitats for the multitude of plant species that provide habitats for the diversity of animals. All of this adds up to a remarkable physical diversity and a much greater biological diversity or "biodiversity," all of which we must do everything possible to preserve.

Virtually every aspect of the intricate web of biotic and inorganic diversity provides an ecological niche that supports one or more species of plants or animals. Each such community which interacts within itself and with its segment of habitat, forms a definable ecosystem. Such ecosystems, at every level of complexity, are what must be ordered and classified so that knowledge about them is made accessible. The resulting classification must serve as a guide to this labyrinthine complexity.

EXISTING SCHEMES OF CLASSIFICATION

As noted above, there is an enormous literature on classification of vegetation, animal communities, ecosystems and, in general, ecological entities. As also mentioned, it would require several books rather than a review paper to digest and summarize this literature. A plethora of terms, maps, and systems have been proposed, and many of these are, or have been, in use. Many of them have value, especially in relation to the purposes for which they were created. Some of these purposes and values are discrepant and even conflicting. No one system of ecological terminology or classification is suitable for all purposes. This view is not, however held by all workers in the field. The extreme opposite position was very positively expressed by no less a person than Professor van Steenis who said (1956 conversation with Fosberg), "there can only be one correct vegetation map of an area."

In this paper it seems only practical to give an idea of the principal systems of very broad, or worldwide application; and of terms and concepts of possible use or significance in formulating a hierarchical classification of ecosystems for use in efforts toward conservation of biodiversity, especially in the Pacific islands. No special effort is being made to be sure of the complete history of a term or even of a system, so long as the concepts are clear and understandable. More attention will be paid to the appropriateness of terms, concepts, and features of the systems discussed for use in the classification to be constructed. A basic aim will be to determine and convey how effective a term or concept will be for storing and retrieving information for the proposed classification of ecosystems. This objective may in places cause the sequence of this paper to be less direct or economical than might be expected.

It is not our purpose here to describe the ecosystems that are classified, but we may properly be reminded that no matter how good a classification is, the results of its use or application will be no better than the quality of the records of the ecosystems, or communities plus environments, to be classified. The recording and description of data on the natural phenomena of vegetation is a whole other subject, but an important and essential one (see Dansereau 1957). Terminology is the connecting link between the descriptive data and the classification, so terminology will frequently be discussed and used in the remainder of this paper. Some definitions will be offered of terms that are not obvious.

We will present three general types of classification schemes. These are:

1. Strict or almost strict vegetation classifications;
2. Ecological approaches to vegetation classifications; and
3. Ecosystem classifications.

Some of the systems discussed in these three sections will be discussed again or referenced during the later presentation of classification units. A later section also covers systems of biogeographic classification as a possible approach to the top level in a classification of ecosystems.

Strict or Almost Strict Vegetation Classifications

The Braun-Blanquet System of Phytosociology: The most widely accepted vegetation scheme, especially in continental Europe, is that developed by Professor J. Braun-Blanquet of Montpellier, France, and associated also with Zurich, Switzerland (Braun-Blanquet 1932, English translation by Fuller and Conard; also see Becking 1957). The Braun-Blanquet system of vegetation science, though usually thought of by those not involved with it as just a scheme of classification, and nomenclature, is actually a well-rounded method of collecting, organizing, and interpreting information on plant cover of areas of the earth's surface. It is only the classification aspect that concerns us here and that most Americans are aware of.

The Braun-Blanquet approach is based on floristic data, which are used as indicators of the associations, the basic unit, and of higher units which are groups of associations. The data for these higher units indicate but are not based on environmental factors. This differs from the usual American indicator concept (e.g., Clements 1902, 1936) in that it does not hold that a single species reliably indicates an environmental complex, but that a number of species together give a more reliable indication. The concept of "fidelity," that certain species are found in no other "association" is central to the system. These faithful species are called "character species." Other species, present, but not exclusively so, are called "constant." A group of species usually found together in the association, and useful in differentiating it from other associations, are called "differential species." The procedure of the method, after the selection of the plots, on which the "relevés," or working building blocks of the system are selected, is a prescribed standard order which, if followed, will yield associations, if such exist in the area of vegetation.

The critical operation in Braun-Blanquet's method is the choice of plots for making the relevés on which the floristic analyses are based. A standard sized area of <u>homogeneous</u> vegetation is chosen <u>subjectively</u>. The data which are abstracted from these plots are the raw material from which the relevés are compiled. The relevés are then tabulated and the associations are derived statistically from the tables. One of the most severe criticisms of the system has been aimed at the subjective, rather than random choice of plots. In our opinion, the careful selection of plots, based on experience with the vegetation is the real strength of the method. If the choice of plots were random, it would be very unlikely that any associations would result from the operation. The association, as stated above, is the fundamental vegetation unit of the system.

These associations are grouped into a higher category called "alliances," by the same method, and the alliances into orders, and the orders into classes. The associations are usually not readily recognizable on quick ground observation, and reading a description of vegetation according to this system gives no visual impression of the vegetation. At the alliance level it is often possible to recognize the units visually in the field, but only after some experience.

The Braun-Blanquet scheme undoubtedly detects and portrays something real, and maps based on it have proven very useful in indicating environmental factors and in land-use planning. However, it is not clear that it would help in defining ecosystems, at least not without a high cost in time and labor. In spite of its wide acceptance, we can ignore it in our present context. We have described it in some detail, informally, because it is so firmly entrenched in the science of phytosociology that strong arguments are possible for its adaptation as the basis for the description of the vegetation component of the ecosystems to be classified. Though a useful scheme, we do not at all recommend it for our purposes (also see Egler 1954).

Dansereau's Scheme: Another system, completely structural and based on features of the plants only, was proposed by Dansereau (1957, 1958). Basic in this system are six features: (a) plant life form (after Raunkiaer 1937), (b) plant size, (c) coverage [%], (d) function (deciduous or evergreen), (e) leaf shape and size, and (f) leaf texture. Each of these is subdivided, the divisions represented by letter symbols. These criteria can be combined to indicate formations. The system is more precise than a strictly physiognomic one, and when used for mapping, can be supplemented by profile diagrams according to Dansereau's (1958, pp. 31-72) formal or symbolic system. The system is useful, and our only objections to it are the use of letter symbols and percentages for cover, and that it does not cover a sufficient range of variables.

Also interesting is Dansereau's (1957, pp 128-131) digest and illustration of del Villar's (1929) ideas, basic to critical consideration of ecosystems. Dansereau's short summary makes it clear that this is an important work, and should be considered by anyone seriously interested in the ecosystem concept.

Küchler's System: Küchler (1949, 1967, 1972) has proposed a structured hierarchical system that accounts for an ample range of observable variables. He calls it a "physiognomic classification," but it is much more than that. It is structural and also functional in Fosberg's sense (see below), and it is very suitable for mapping, if a legend is provided. Our main objection is that it is expressed in letter symbols and formulae rather than names and diagnoses, therefore giving no visual impression of the vegetation. His main subdivision is into woody versus herbaceous. This presents inherent difficulties in dealing with massive succulents and other acaulescent xerophytes, giant herbs such as Musaceae (sensu stricto), and lianas or climbers. This scheme or a modification of it may well be useful in our discussions.

Fosberg's Scheme: In the 1950's, Fosberg's studies of tropical island vegetation directed his attention to possibly appropriate terminologies and classifications to use in placing on record the vegetation information acquired. Most of the existing systems had been developed in the temperate zones and were less well-suited to tropical vegetation. Most systems also involved environmental features, especially climate, soils, and available water, in addition to or even in place of the vegetation itself.

Fosberg experimented with possible methods of using only features of the plants and vegetation. Over several years he developed versions of a scheme utilizing what he called "structural and functional features" of the vegetation (1961a, 1961c, 1967). The difficulties were apparent in dealing with aquatic vegetation and terrestrial vegetation in extreme situations such as on cliffs and in deserts. Environmental implications crept in, especially into the terminology. A final version of this classification was included in IBP

Handbook No. 4, of the IBP section of Conservation of Terrestrial Biological Communities (Fosberg 1967).

The primary subdivision in this system is the spacing of the plants, i.e., closed, open, or sparse. Spacing is estimated by a visual method not involving percentage cover. The three units at this level are called "primary structural groups." Under these are "formation classes" and in these, "formation groups." The basic category, then, is the "formation" under which there may be "subformations" if needed. The classification goes no further, as any further subdivisions would be on floristic composition, which is impractical on a world-wide scale.

Fosberg attempted to construct a classification that will work where only a minimum of information is available, but which is adaptable and capable of further subdivision by using modifiers with the terms when more adequate information becomes available. Fosberg avoided the term "cover" in its usual sense, as it implies the (usually impractical) measurement and determination of percentages. He also avoided floristic information, though that can be added in a modifier sense. Floristic information is mostly useful in establishing "associations" which form a lower level than Fosberg's classification includes. Finally, he also avoided terms which end in "land," as these imply habitat and are broader than a strictly vegetation sense. This suffix may well be added to convert higher level vegetation units into ecosystem units, e.g., grassland, woodland, shrubland, etc.

The Fosberg system has been compared with the UNESCO (1973) classification by Goldsmith (1974) showing that each has its advantages and weaknesses. It should be noted that Eiten (1968) has developed and proposed a major revision and amplification of the Fosberg classification, resulting from his extensive experience in Brazil. He has introduced much detail and more precision. Anyone proposing to use Fosberg's system for more than casual vegetation work would do well to give serious attention to Eiten's paper.

The USFWS Structural Classification: A new and very different classification has been proposed by the USFWS prepared at the Thorne Ecology Institute, Boulder, Colorado, available in duplicated form only (Moir et al. 1988). It is a classification of terrestrial vegetation, based on structural features only. It is supposed to be a step forward from the Dansereau, Küchler, and Fosberg schemes, especially suitable for temperate zone vegetation, and easier to use by workers with little or no botanical knowledge. The aim of the authors was "to produce a structural classification of terrestrial vegetation with particular application to North America, but also intended to apply worldwide."

The authors have abandoned names for their units, below the top rank of "major structural groups," of which there are eight: forest, woodland, scrub, dwarf scrub, herbaceous vegetation, nonvascular plant vegetation, and barren. These are defined mainly by percentages of different growth-forms. They are subdivided into up to 10 different defined "ranks," designated by numbers, modified by "descriptors" or characters of vegetation structure. "A descriptor is a class of objects that exist in discrete conditions. Each descriptor has been partitioned into mutually exclusive subclasses, or "states." Each state has a letter code followed by a word or "phrase."

A glossary is provided, which gives special, often lengthy, frequently unfamiliar, definitions for most of the important words used in the classification and text. The user will get nowhere until he has thoroughly familiarized himself with this glossary. A list of references cited is given, with familiar and unfamiliar authors and papers, also with surprising omissions.

This work seems to be an almost total departure from traditional vegetation concepts and classifications. There is no doubt that if properly applied, a useful and valuable mass of information on vegetation would be accumulated. One would not know what to call the units. Many definitions are in terms of percentages, perhaps giving a false sense of precision. Special uses of familiar terms create confusion.

One item Moir _et_ _al_. bring out in their introduction is the fact, usually neglected or ignored, that standing and fallen dead trees, rotting logs, and other dead remains are still part of the vegetation. This is a somewhat controversial matter, though Fosberg has long agreed with it, particularly concerning peat and mor. Dead material is certainly an important part of the ecosystem.

Our comment on this classification is that it is an interesting departure, but that it is not likely to contribute much toward the task of arriving at a suitable classification of ecosystems.

Ecological Approaches to Vegetation Classifications

The systems reviewed above are more-or-less true vegetation classifications, the features used as criteria being those of the plants - the plant species or the plant aggregations. Only a few classifications come even close to resting on plant characters only. With only one exception (Braun-Blanquet) among the systems examined, environmental features have crept in, especially in defining units of vegetation in extreme habitats. Most self-styled vegetation classifications are based partly on environmental phenomena. Many of these are perfectly sound systems, but must be regarded as ecosystem rather than vegetation classifications, since they include both organisms and their environments.

It is hard to say who started to classify vegetation in terms of the ecological factors that theoretically control its form and distribution. Grisebach (1872) is said to have established the "formation" category, basic in most physiognomic and structural systems. His book was on the role of climate in classification of vegetation, and it had much to do with the direction of subsequent work. Schimper (1898) firmly established this tradition (see below) which has dominated much of the non-Braun-Blanquet vegetation study, and probably should be referred to as "geobotany."

In earlier pages we have commented on the use of vegetation in establishing the spatial or geographic limits or boundaries of natural, especially major, ecosystems. We can only summarize some of the high points and mention several important works in the vast literature on geobotany or ecological vegetation study, but must point out that this work is basic in what we are working on, no matter whether the subject matter is called "vegetation" or "ecosystems." It is a pity that so many of the important works are in German, making it hard work for us linguistic semi-literates to read. Fortunately a few of these, especially Schimper, have been translated.

Schimper's System: Schimper (1898) devoted the greater part of his huge book to details of the ecological, geographic, and especially climatic relations of vegetation on earth. Little that was known in these fields in his time was neglected by him. Even now, almost a century later, there are many days of profitable reading in Schimper's big book for anyone with ecological interests.

For our purposes his Part II, Chapter 1, on Formations and Guilds, is most pertinent. He groups vegetation into three vast categories: woodland, grassland and desert. Already he has established that he is writing about ecosystems, though the term and the concept had not yet been invented. Those three groups of formations he believes are due to regional climate. Subordinate to his climatic formations, he proposes "edaphic formations" due to "differences in the physical and chemical nature of the soil." His discussions in this chapter occasionally sound quite anthropomorphic, as he is clearly trying to show a large and probably unscientific audience his conclusions. He proposes, or uses, many terms which have become well-established in ecological parlance, e.g., xerophyte, lithophyte, chasmophyte, psammophyte, etc.

Schimper, although he did much to establish the formation concept, and provided great amounts of description of formations, did not systematically classify and characterize his formations. He had too much fascinating information about them to settle down to organization and routine description. He left that to his numerous, mostly German and Swiss followers. He was obviously much more interested in the remarkable phenomena that he observed and interpreted than in classification and terminology.

Schimper's Successors: Von Faber, co-author of the great third edition of Schimper's book (Schimper and von Faber 1935), organized the formations into 15 "formation types" (termed formation classes earlier by Rübel (1930) and also by most subsequent authors), and prepared a world map of these, redrawn later by Dansereau (1957). Rübel recognized only nine formation classes; Dansereau, following Schimper and von Faber, recognized 15; Küchler 32, Fosberg 31, and Schmithüsen eight with many subclasses. These are clearly not really comparable or equivalent.

Schmithüsen (1968) gathered an enormous compilation and interpretation of the "vegetation" information that has any geographic or landscape interest. This major work summarizes the geographic and ecological information available in his time, albeit in complicated German. It is far too detailed to even summarize here, or for our purposes, but will, for a long time, be the major reference in what we are calling geobotany, as well as in much of ecology.

The UNESCO Classification: In 1969, a physiognomic classification of world "vegetation" was published, prepared under the auspices of the UNESCO Standing Committee on Classification and Mapping of Vegetation on a World Basis (UNESCO 1969). This, as with so many other "vegetation" classification and mapping schemes, was not strictly based on vegetation features, but included environmental criteria, and must, on a strictly logical basis, be called an "ecosystem classification." This system was revised and republished in 1973 by Heinz Ellenberg and Dieter Mueller-Dombois as International Classification and Mapping of Vegetation (UNESCO 1973), and is sometimes referred to as the Ellenberg or Ellenberg and Mueller-Dombois system (e.g., Goldsmith 1974).

This is a hierarchical scheme with units in five levels of subdivision: formation class, formation subclass, formation group, formation, and subformation with provisions for further subdivisions where necessary. Its first subdivision, on the basis of stature and spacing, divides vegetation into five formation classes:

I. Closed Forest;
II. Woodland;
III. Scrub;
IV. Dwarf Scrub and related communities; and
V. Herbaceous Vegetation.

Each of these, and its subdivisions at four or more levels, is given a phrase name and/or a diagnosis, separating it from its related coordinate units. The criteria used are, where convenient, such features as evergreen or deciduous leaves, growth form, leaf shape and texture, and such environmental features as altitude, dryness, seasonal rhythms, habitat, and whatever may help to recognize or distinguish the units. In many cases, examples are added which help greatly in visualizing the units. Each unit described is given a serial numerical designation and a distinct formula (e.g., II.A.2.a.(1) following traditional outline format). The example code indicates "Evergreen needle-leafed woodland with rounded crowns with evergreen sclerophyllous understory."

This is not perfect, but it seems to be the most satisfactory terrestrial ecosystem classification yet proposed. It is included in essentially its original form in the Mueller-Dombois and Ellenberg volume on vegetation ecology (1974).

The IUCN Classification: In the same year (1973) that the UNESCO scheme appeared, IUCN published "A Working System for Classification of World Vegetation," which is a simplified and shortened version of the UNESCO effort. It uses a more familiar, vernacular terminology for naming its units, and combines some similar units from the UNESCO system. It is really three parallel classifications, one for tropical and subtropical vegetation, one for humid and sub-humid temperate and sub-polar regions, and another for deserts, sub-deserts, wetlands, and aquatic formations. This scheme is undoubtedly easier to use in the field, and for most purposes is satisfactory, though not designed to record as much detail as its parent UNESCO system. It does not provide for the more minor floristic systems at the association level and lower, a shortcoming shared almost by definition with every other world scheme except that of Braun-Blanquet.

Daubenmire's System: In 1978, R. Daubenmire proposed a system of plant biogeographic regions for North America. His system begins with biogeographic regions based on climatic vegetation climaxes. The next level is the "province" within which geologic history is relatively uniform and plant taxa are historically related. The next level is the "zone" within which macroclimate and soil groups are generally uniform. Finally, the fourth level is "habitat type" based on potential natural vegetation.

Ecosystems Classifications

Since the concept of "ecosystem" is a relatively new one, and one that for years has either been widely ignored or misunderstood, only a few classifications of these systems *per se* have been developed. A few of these will be briefly considered here, including the earliest, by A. B. Klugh, and later efforts by V. Krajina, and H. Ellenberg. We will also introduce two wetland ecosystems classification systems, and finally, give a brief account of the classification challenge of subterranean ecosystems.

Klugh's System: In 1923, A. B. Klugh briefly reviewed the subject of ecological classification and proposed a "Common System of Classification for Plant and Animal Ecology." This scheme which includes marine, fresh-water and terrestrial ecosystems depends almost entirely on environmental criteria, seems one of the best attempts to classify habitats of both plants and animals. It is rather general for our purposes, but deserves serious consideration. It has not been widely used, possibly because it introduces and uses many new or totally unfamiliar terms. It does account for practically every existing ecological situation that was known in 1923.

Krajina's System of Biogeoclimatic Zones: Working on the ecology of British Columbia, Professor Krajina (1965) designed a system of what he termed "biogeoclimatic zones" (Mueller-Dombois and Ellenberg 1974, pp. 166-168). He defined a biogeoclimatic zone as a geographic area that is predominantly controlled by the same macroclimate and characterized by the same soils and same zonal (climatic climax) vegetation.

The term "zone" which is common in the literature of soils and, to some extent, of vegetation, is elusive, varying somewhat with the particular writer. It seems generally to imply a geographical phenomenon controlled by limiting habitat factors. When these vary continuously, local phenomena of vegetation or animal community belts (along altitude, moisture, or other gradients) may develop (e.g., Holdridge 1947, 1967). When these factors vary discontinuously, a mosaic of zones may develop. While the former type is typically fairly small, the latter may be quite large as in Krajina's system.

Krajina included within his biogeoclimatic zones the biogeocoenoses of Sukachev. The aerial extent of a biogeocoenosis is determined by the extent of the phytocoenosis, which is a rather narrowly defined and mappable plant community. Krajina's system is very useful for the study of major ecosystems. It's main advantage and obstacle to application is the diversity of data that must be collected to classify its ecosystems. This range of data is not ordinarily within the competence of an individual ecologist.

<u>Ellenberg's Classification of World Ecosystems</u>: H. Ellenberg (1973), based on a lifetime of experience as an ecologist, proposed a comprehensive, hierarchical scheme for world ecosystem classification including phenomena and concepts that, though obvious and important, have rarely been included in other classifications (e.g., the influence of human activities).

The hierarchy starts at the top with the all-encompassing world ecosystem, or "biosphere." This is subdivided partly on the basis of the energy sources utilized: the sun for natural or predominantly natural ecosystems; and "reconstituted energy" or fossil fuel or atomic energy for "urban-industrial" ecosystems. Note that a modern system would have to include the chemical energy-based natural ecosystems of the oceanic thermal vents. Another criterion used by Ellenberg is the life medium. This second level includes five divisions or "mega-ecosystems." These are marine (salt water), limnic (fresh water), semi-terrestrial (wet soil and air), terrestrial (aerated soil and air), and urban-industrial (human-created) ecosystems (including agro-ecosystems?).

"Macro-ecosystems," the next level, are based on productivity - consumer - decomposer phenomena and the factors regulating these processes. "Meso-ecosystems" make up the next level, and are considered the most basic units of the scheme. A meso-ecosystem is composed of a relatively uniform or homogeneous abiotic system plus its characteristic life forms functioning as primary and secondary producers. "Micro-ecosystems," the next level of division, are characterized by distinguishing natural features or life-forms. Each "nano-ecosystem," at the next level, is unique, and is characterized by its particular natural features and species.

The definitions of the units at each level in the terrestrial branch of the hierarchy are characterized primarily by vegetation according to the UNESCO structural-ecological formation system (UNESCO 1973), so the meso- and micro-ecosystems correspond more-or-less to vegetation formations and sub-formations. Ancillary subsystems at the various levels form a part of Ellenberg's overall scheme, but are not part of the hierarchy. These subsystems allow for additional refinement of ecosystem data. A category of subsystems such as layers, resource-sharing groups (synusiae or guilds), substrate inclusions, and "pheno-partial" or seasonal manifestations is provided for use at the meso- and micro-ecosystems levels. Another category of subsystems operating at the top level provides for identification of nine biogeographic regions, facilitating world-wide comparisons of lower level units. Still another set of subsystems is a scale of four levels or degrees of human interference with natural ecosystems. These include:

1. Harvesting of organic materials or minerals that are significant for the functioning of the ecosystem;
2. Adding organic or inorganic materials to the ecosystem;
3. Toxification, or adding substances to the ecosystem that are deleterious to its functioning or to that of its important component organisms; and
4. Changing the species composition by suppressing or causing the extirpation or extinction of existing species or by the introduction of alien species to the ecosystem.

This Ellenberg scheme is based entirely on structural and functional characteristics. Its usefulness obviously is proportional to the thoroughness with which an ecosystem or system of ecosystems can be described. As the most fully elaborated system for classifying ecosystems, it should be seriously discussed in any effort to develop a scheme for the classification of ecosystems. Its utility for conservation evaluation should be apparent.

The USDA Forest Service "Digitized" System: One of the strangest ecosystem classifications recently proposed was offered by Brown et al. in 1980. This system is intended to allow the USDA Forest Service to computerize information about ecosystems classified in a hierarchical way. The system begins with "biogeographic realms" (after Wallace and Udvardy) at the top level, and descends through "vegetation" (actually substrate) characterized by topographic position and available water, to formation type (e.g., grassland), then to climatic zone (potential natural vegetation), then to biome (apparently in the sense of sub-formation), and climax series (plant growth-form), in that order. This hierarchy scarcely seems hierarchical, or for that matter, sensible.

Wetland (Wet-terrestrial) Systems

The USDI Fish and Wildlife Service Wetlands Scheme: The USDI Fish and Wildlife Service (USFWS) must cope with the difficulties of classifying aquatic or wetland habitats. That organization is required to maintain an inventory of the wetland resources of the United States. This was first established according to a scheme set up by Martin et al. (1953) that was relatively simple, but not altogether internally consistent nor complete. This scheme was created to be used as the basis for inventory and analysis of wildlife habitats.

Recently, the great importance of wetlands began to be realized, even by the intelligent lay public, and the necessity for a new and up-to-date inventory of wetlands per se became evident. The old paper by Martin et al. (1953) was no longer considered adequate for a proposed inventory, so the USFWS Office of Biological Services set up a project under Lewis M. Cowardin, who with three colleagues, Virginia Carter, Francis C. Golet and Edward T. LaRoe, undertook to produce a classification that would serve all of the agency's purposes. This was first published in 1977 and somewhat revised and reprinted in 1979 and 1985. It has been officially adopted by the USFWS and other US federal agencies for all of their wetlands classification, inventory, and regulation activities.

Cowardin et al. (1985) produced a classification of wetlands that accounts for almost every imaginable saturated or seasonally saturated environment. Applied properly, each unit can be described in almost every significant detail. The problem of assigning names to the units is avoided completely. All are called "wetlands" with a series of refining and modifying terms or codes.

The most obvious first breakdown might be between wetlands and deep-water habitats, but this separation does not enter the classification. The highest level in the classification is a series of five "systems" based on the character and occurrence of the water in each system. There are marine, estuarine, riverine, lacustrine, and palustrine systems. In other words, there are oceans; estuaries; rivers and streams; lakes and ponds; and swamps, bogs, and marshes. Ten "subsystems" form the next level based on water level and tidal behavior and the permanence of saturation. A still lower level of "classes" (one to eight per subsystem) is based on the nature of the bottom and on the biota. Classes may be further modified by additional codes for appropriate features.

As stated above, this scheme can account for any imaginable saturated situation. Many of the units have no defining biological characteristics, though microorganisms and cryptic forms are doubtless present. The units at all levels can be considered to be ecosystems and might be useful in our attempt at classification except that there seems to be no simple way to refer to them (a common problem of many of the schemes discussed here).

Some of the systems of wetland classification that this scheme was created to replace were much simpler and had named units, but the problem was that they did not account for all of the kinds of wetland ecosystems. The choice, as often happens, is between the simple and inadequate and the complex and impractical. The Cowardin system and its predecessor were set up to take inventory of US wetlands. For our purposes, a selection might be made of aquatic ecosystems that include different biotas and that occur on islands. Whatever scheme is tried, it will not be both simple and adequate.

The Canadian Wetland System: Another wetland classification system has been proposed for use in Canada (Zoltai et al. 1975). This system utilizes only three levels. The first of these is "class," which seems to be based on vernacular formations (e.g., bog, marsh). The second level is "form," which has to do with the surface morphology of the wetland, soil type, acidity, water table position, etc. Finally, the "wetland type" is characterized by the physiognomy of dominant plant species.

Subterranean Ecosystems: A review of the literature on caves and subterranean ecosystems failed to yield anything like a comprehensive approach to cave ecosystem classification. Sweeting (1973, p. 158) classified karst caves as phreatic (above the water table, basically dry), vadose (caves containing running and/or standing water but not submerged), and vertical. Ford and Williams (1989, p. 243) listed thirteen factors for the classification of caves including size, shape (3 variations), relation to water table, rock type, mode of geological control, topographic setting (2 variations), role in the fluvial system of the region, porosity of the aquifer, relative activity of development (active versus relict), and climate. No classification of caves in igneous or metamorphic rocks nor of caves in tropical karst landscapes was encountered.

Under the circumstances, we might choose a few factors, perhaps to include rock type (limestone, other sedimentary rocks, basalt, andesite, other igneous rocks, metamorphic rocks), water type (salt, fresh, coastal mixing), water regime for fresh water caves (e.g., xeric and mesic in the phreatic zone, vadose) and topographic setting (e.g., montane, coastal, lowland, makatea) as an experimental basis for classifying caves.

MAJOR REVIEWS

We should not end this part of our account without mentioning, again, a few major reviews that bring together at least a substantial selection of the literature that has grown up around vegetation. Vegetation is an omnipresent phenomenon, so complex that no one completely understands all of its aspects. It is naturally excessively written about.

Schmithüsen's book on geobotanical classification, described above, gives one the feeling he would get from reading a street and business directory of New York City. One is amazed that anyone could have a grasp of such a labyrinthine collection of facts, and make sense of it, as Schmithüsen has.

On a more modest scale, but impressive none-the-less, are sections in two books. Mueller-Dombois and Ellenberg (1974) have effectively summarized many of the principal vegetation classifications, bringing together in an organized and readable fashion much of what the ecologist or vegetation scientist needs to know. Dansereau (1957) has done the same in a different manner, interpreting principal aspects of plant geography in ecological terms and principles. These two books should be an essential part of the training of any aspiring vegetation scientist. Also see Shimwell (1972).

Animal communities, too, have received much attention, but less of this topic has been treated as generally as have plant communities. Most attention by zoologists and animal ecologists has been to what botanists call "autecology" - the behavior and ecological relationships of individual species, and particular relations between species. The range of interrelationships among animals has been written about, but is more elusive, the communities are less tangible, and the individuals sometimes run away and hide.

An outstanding attempt to generalize the animal aspect is the book on animal communities by L.R. Dice (1952). He wrote with great understanding in a wide field, but one does not get the feeling of being overwhelmed by the mass of information as one does in reading comparable works on vegetation.

Perhaps the most comprehensive reviews of biotic communities in English are Whittaker's 1962 and 1975 summaries of what is known of natural communities. These are truly comprehensive, organized, clear presentations of a tremendously complex subject. They tend to be more satisfactory on the vegetation side, being written by a botanist, but their frameworks integrate both major branches of community science.

CLASSIFICATION UNITS FOR ECOSYSTEMS

Some attention must now be paid to the nature and terminology of the ecosystem units to be classified and their levels in the hierarchy. Selection of designations for units is complicated by the necessity, in our ecosystem classification, to use terms for biotic communities, that is, those including both plants and animals. Terminology of plant or animal communities is usually available, especially for the former; in fact some feel that plant ecology is overburdened by its vocabulary. But terms for different levels of biotic communities, especially unambiguous ones, are less easy to find.

The term "community" itself, unqualified, should be defined without ambiguity. It should ideally mean an aggregation of interacting or interdependent organisms occupying a habitat. It has been much more frequently used for plants only or animals only, so perhaps where it makes any difference, the term "biotic community" should be used.

At the highest level of generalization, which also comprises the broadest geographical areas, there is easiest and most general agreement. This divides the earth's surface into land and water (some of it frozen), coordinate with the aquatic and terrestrial divisions of the globe's surface.. There seems to have been little problem of controversy here, except on the boundary zones between the two. Some land is periodically dry or inundated. This and the land where the emergent plants are rooted below water level, are by different schemes included as either land or water. By some authors these are separated out into a catch-basket called Azonal.

Conceptual Discussion of Levels in the Hierarchy of Ecosystem Classes

An endless series of terms have been proposed and used to designate the kinds of units and the ranks or levels in which they are placed in classifications and mapping systems. Some of them may be appropriate for our purposes, but the great majority must be ignored, lest they lead to book-length discussions. We discuss a few of the most important ones. We will begin with a review of some of the more important biogeographic regionalizations. We will then consider the following: biomes, formation classes, formations, subformations, and associations, which are abstract (type or collective) terms. Concrete (actual) ecosystems may be called biomes, communities, associations, societies, regional communities, stands (ecotopes), and microstands. Distinguishing between terminology for types and actual occurrences is critical. We will recommend resolutions for the dual usages of "biome" and "association."

Major Biogeographic units

Biogeographers generally subdivide the terrestrial areas of the earth into major divisions, the names and boundaries of which have varied enormously according to different authors, from Schimper, Wallace, and Humboldt (the founder of biogeography) to Dansereau, Udvardy, and Bailey, among the most recent authors of world-wide systems.

Humboldt proposed the first scientific set of biogeographic regions based on the distribution of physiognomic vegetation formations controlled by climate (1805, 1806). We have already discussed Schimper's (1898) vegetation regions. In 1876, Wallace proposed the first scheme of zoogeographic regions, based primarily on Humboldt's work. Wallace intended to further develop his system on the basis of animal interactions with their environments, but he could not fully develop this idea with the data available, so he developed a system of natural regions based on the origins and extents of animal distributions (and in the process invented a new field of biogeography) (Rotramel 1973).

Udvardy's Biogeographic Provinces: Udvardy (1975, 1984), elaborating on Dasmann's (1973, 1974) tentative scheme, divided the terrestrial part of the earth into eight zoogeographic "realms" each subdivided into "biogeographic provinces." The Oceanian Realm includes the Papuan, Micronesian, Hawaiian, Southeastern Polynesian, Central Polynesian, New Caledonian, and East Melanesian Biogeographic Provinces. He is presently working on a complete revision and elaboration of his 1975/1984 system.

Takhtajan's Floristic Regions: Takhtajan (1986) published a volume on the Floristic Regions of the World considerably updating the older system by R. D. Good (1947, 1964) which included four levels - kingdom, sub-kingdom, region, and province). Takhtajan divided the earth's surface into six kingdoms (e.g., the Paleotropical Kingdom), several subkingdoms (e.g., the African, Madagascan, Indomalesian, Polynesian, and Neocaledonian Subkingdoms in Paleotropis) and 35 floristic regions. In the Pacific, these include the Malesian, Fijian, Polynesian, Hawaiian, and Neocaledonian Regions in both the Indomalesian and Polynesian Subkingdoms. Regions may be subdivided into subregions (e.g., the Malesian and Papuan Subregions in the Malesian Region), and all regions (or subregions) are then subdivided into provinces (e.g., the Celebesian, Moluccan, Papuan, and Bismarckian Provinces in the Papuan Subregion).

Dansereau's Biochores: The most inclusive major unit that might be considered an ecosystem is the "biochore," as treated by Dansereau (1957), which is based on a combination of climatic factors and very general structural features of the vegetation. Each biochore includes a number of "formation classes" (sensu Rübel 1930) (equivalent to the formation types of Schimper and von Faber 1935). Although the biochore concept has not been widely used, it seems to be a real high-level ecosystem, and of great interest.

Bailey's Ecoregions: For a number of years, R. G. Bailey of the USDA Forest Service has been working toward a system of "ecoregions." Bailey's Ecoregions of the United States was published in 1976 (map) and 1980 (descriptions) (and revised by Omernik in 1987). In 1986, Bailey and Hogg published a prospectus for "A World Ecoregions Map for Resource Reporting," and in 1989, Bailey published his Ecoregions of the Continents. An ecoregions map of the oceans is in development.

These ecoregions are based on climate (after Köppen 1923, 1936 and Thornthwaite 1933) and vegetation, broken down in various ways, and applied in such a way that areas with various features form correlated wholes. Four hierarchical levels are recognized. At the top are the Polar, Humid Temperate, Dry, and Humid Tropical Domains. The domains are subdivided into 15 primarily climatic "divisions," in each of which there may be either one or two "regimes" (mountains and/or lowlands). The divisions (and regimes) are subdivided into ecoregions on the basis of vegetation, of which there are 101 on the terrestrial surface of the earth.

Whether these ecoregions are intended to be equivalent to biomes (discussion below) is not altogether clear; but the subdivisions result in more ecoregions than there are generally recognized biomes. There is little doubt that Bailey's and Omernik's ecoregions are natural, very large ecosystems. They should be considered in any essay toward the classification of ecosystems.

Biogeographic Units in the Pacific

Four authors have published biological or ecological regionalizations of the insular tropical Pacific. Three of these are based more-or-less on flora and vegetation (Fosberg 1957a, 1957b), birds (Mayr 1940), or terrestrial animals (Curry-Lindahl 1980a, 1980b). Only one deliberately includes environmental factors. Dahl (1980) includes island form and origin and climate as well as distribution of species and communities. The insular segregation of these units precludes considering them as large scale ecosystems, unless the marine components are considered and discovered to provide system-wide connections.

Mayr's Polynesian Region: At the sixth Pacific Congress (Berkeley 1939), Mayr presented a paper entitled "Borders and Subdivisions of the Polynesian Region Based on our Knowledge of the Distribution of Birds" (Mayr 1940). Mayr defined the Polynesian Region as the tropical islands of the Central Pacific east of the Philippines and Japan, west of the Galapagos, and north of New Zealand. New Guinea is considered to be a separate subregion, leaving a Polynesian subregion including the following divisions: Micronesia, Central Polynesia (west of 165° W. longitude through Fiji), Eastern Polynesia (east of 165° W. longitude), and Southern Melanesia (Santa Cruz and Banks groups, New Hebrides, Loyalty Islands, and New Caledonia).

Fosberg's Vegetation Provinces of the Pacific: In 1953, Fosberg presented a characterization of the vegetation provinces of the Pacific to the eighth Pacific Science Congress (Quezon City) (Fosberg 1957a). There were 21 Provinces defined for the Indo-Pacific Region including its continental margins. One of these was the Oceanic Province including all the true oceanic islands of the tropical Pacific except Hawaii and the Galapagos (in provinces of their own), and also excepting the atolls of Melanesia. Other provinces with which we will be working include the Papuan and Melanesian Provinces. A separate paper presented at the same congress described the vegetation of the Oceanic Province (Fosberg 1957b).

Curry-Lindahl's Zoogeographic Subregions of the Pacific Realm: In 1980, Kai Curry-Lindahl published a two part article in Environmental Conservation on the zoogeographically defined subregions of the Pacific realm. This paper had originally been presented to the 13th Pacific Science Congress (Vancouver 1975) and was apparently an attempt to refine Udvardy's biogeographic provinces in the region. Continental margins are excluded, but marginal archipelagos are not. Curry-Lindahl defines four regions (northern, western, central, and eastern) with the central region including five subregions (Hawaii, Micronesia, Melanesia, Polynesia, and Easter Island - Gomez).

Dahl's Pacific Biogeographic Provinces: In 1980, based on work ongoing for several years and with the support of the South Pacific Commission and IUCN, Arthur

Dahl published a Regional Ecosystems Survey of the South Pacific Area. The first part of the volume presents a breakdown of the insular Pacific into 20 biogeographic provinces. These tend to coincide almost exactly with archipelagos, and thus have considerable biological validity (as an artifact of dispersal and evolution), but they cannot reasonably be considered as ecosystems.

Dahl's biogeographic provinces were heavily influenced by the divisions of the three authors listed above and by Fosberg's "Biogeoclimatic Patterns in Micronesia" (13th Pacific Science Congress, Vancouver, unpublished) and G. Carleton Ray's "Preliminary Classification of Coastal and Marine Environments" (1975, since refined in Ray et al. 1984; Hayden et al. 1984). This last influence insures that Dahl's biogeographic provinces are not exclusively terrestrial.

Major Ecosystem Classification Units

The Biome: The largest widely accepted, definable terrestrial ecosystems are those to which the term "biome" is often applied. There does not seem to be much real agreement on defining this term or on either the breadth or degree of uniformity required in its components.

The biome concept was first proposed by animal ecologists (Kendeigh 1954; Odum 1945; Shelford 1913, 1932, 1963) as a major biotic community, but biomes are distinguished and recognized by their vegetation physiognomy. Whittaker (1962, p. 70) and Dahl (1980) even equate the term biome with formation. Whether or not a biome is necessarily a continuous area or can comprise all similar areas on a continent, or even in the world, is not agreed on. The term "major ecosystem type" has been used synonymously with biome. For the purpose of ecosystem classification, the following abstract concept seems most satisfactory: a biome is all members of a broad community complex marked by vegetation of similar physiognomy and with faunas adapted to the environment that supports and includes these vegetation types. This definition would place all temperate broadleaf deciduous forests in a single biome, or all coarse-leafed tropical grasslands and savannas, or all arctic tundra, or all mangrove swamps, or all cloud forests, or all montane-rain-forests. A biome is thus an ecosystem type. Probably any hierarchical classifications of ecosystems should have the biome or an equivalent concept as the highest level in its hierarchy.

Merriam's Life Zones: An alternative system might be life-zones, exemplified by the C. Hart Merriam scheme (Merriam 1898, also see Daubenmire 1938), eminently satisfactory for western North America, but difficult to use elsewhere.

Holdridge's Life Zones: Another life-zones scheme is the ingenious Holdridge scheme (1947, 1967), theoretically applicable everywhere, widely used in Latin America, but, strictly applied, requiring better climatic data than are usually available. In Latin

America, where such climatic data are generally lacking, Holdridge and his disciple, Tosi, have admitted to Fosberg that their recognition of these units is by the tree species known to be characteristic of the unit (also see Holdridge and Tosi 1972). Fosberg's experience with this scheme has been that where the required data are available, the vegetation is physiognomically about what is expected, except that transition types seem more prevalent than the main units. His scheme has not been widely accepted and may not be useful outside the northern neotropics, where it was developed.

Australian Land Systems: We must not neglect to mention, though briefly, the system of land survey and classification developed by C.S. Christian at the Australian CSIRO, and very widely used in Australia and New Guinea (e.g., Christian 1959, Christian and Stewart 1968). Survey teams of a botanist, a soils scientist, a geographer or climatologist, and others as needed, make a very broad field sampling of a large area. Their data are integrated into a landscape classification scheme of "land units" grouped together into "land systems."

All in all, the concept of biomes, as described in this section, seems the most satisfactory, in spite of the disagreement and confusion surrounding the term. The fact seems to be that confusion has grown up around every important synecological term. In general, the only safe way to insure understanding is for us to define our terms according to the way we use them.

Subsequent Ecosystem Classification Units

Formations: "Formation" is, at the same time, one of the most useful and definable, and yet one of the most variously misused and ambiguous terms in ecology. In geology it is used in a limited, well-defined sense, and also casually or colloquially for any feature that attracts attention. Both senses have their uses in facilitating communication.

In ecology there is no such agreement, but still, the term can be defined and the vegetation to which it is applied can be visualized. While it has generally been considered to apply to vegetation, it also may be useful in describing the vegetation component of an ecosystem. Restricted to its physiognomic, or more precisely, to its structural-functional sense (discussion below), it is essential in indicating and circumscribing major ecosystems at the next principal level below the biome. Vegetation composed of a majority of individuals with a given growth-form or category of growth-forms, in other words, a formation, is assumed to indicate the occurrence and circumscription of a definable major ecosystem with reasonably uniform components, at a rather broad level of generalization. Variations of this but not differing seriously may be called "subformations."

Dansereau (1958 pp. 17-27) has given us a useful essay toward a classification or grouping of vegetation formations, strictly on the basis of structure, the physical features of the plant aggregations. He sets up a series of ten "formation types" that are certainly logical and recognizable with familiar English word designations. From his discussion (p. 18) it seems that he regards these as "kinds of formations," but later on he seems to consider these also as formations *per se*.

He excluded the term "formation class" from this hierarchy and applied it to what he terms "regional climaxes," of which he enumerates and describes fifteen. These, though he refers to them as vegetation, seem, from his terminology, to include major environmental factors in their conceptualization. They correspond fairly well to the units which we call biomes, above, though they seem a bit broader than what are called biomes by some writers.

Fosberg (1961a, 1961c, 1967) adopted some of Dansereau's concepts, but modified his terms somewhat. Fosberg differentiated what Dansereau calls "structure" into two concepts, structure, involving spacing, stature, and stratification, and function, including morphological features of presumably adaptive significance - modifications such as thorniness, leaf reduction and texture, succulence, and the like. He kept the term "formation" in what seemed its traditional and most useful sense, a physiognomic unit more clearly defined by a combination of structural and functional features.

Higher levels into which the Fosberg formations fall are termed "great structural groups," based strictly on spacing, "formation classes," based mainly on stature, and "formation groups," rather than the more ambiguous "formation type," based on seasonality and deciduous or evergreen character.

It must be reemphasized that the IBP (Fosberg 1967) classification is strictly a vegetation system, artificial in nature, and deliberately avoiding implication of habitat, environment, or dynamics. These can be included, if needed, when the vegetation is used as an indicator of an ecosystem.

Associations: It is at the association level, however, that ecological and vegetation terminology have fallen into a hopeless semantic morass. "Association" as a term has been used at every level from the biome to the mini-stand. It has been defined in a plethora of ways. We would suggest that, as a vegetation term, association be limited to phytosociological use, for units determined by strictly prescribed methods in the Braun-Blanquet system and its modifications. This is its most widely accepted use and is well-understood in that sense. Ideally the term "association" should be discarded by other ecologists, or these workers should provide a definition when they use the term. Unfortunately, a new term for this level of description and classification is not readily available, so we recommend its use for the time being. For the purposes of an ecosystem classification, the term "association" or its alternative should be defined as a recurring group of dominant or conspicuous organisms, plant and/or animal, inhabiting a recognizable and specific habitat type.

Other Infra-formation Categories: For the next level in our hierarchy, we are left without a formal category, and, indeed, perhaps without a set of comparable communities that may be logically grouped, at that level. On a regional basis, a consistent and comprehensive ecological classification is daunting. Island floras and faunas have, in their long histories diverged to such an extent that equivalence, from one to another, can no longer be established, except in an artificial fashion.

For our special purposes, on oceanic islands, there are not many biotic recurring equivalences, even at a generic level, that are convincing, though a few such can be pointed out, e.g., Metrosideros forests, Rhizophoraceae forests, Tournefortia scrub or forest, Scaevola scrub, Cyathea forests, sooty tern rookeries, Pisonia forests, Lepturus grassland and savanna, Miscanthus savanna, etc. More common, especially in uplands, are mixtures, but these merge into each other so as to be not easily classifiable. Classification is possible on an environmental basis using micro-climate, landform or physiography, available water, exposure, elevation, soils, rock-types, etc. Correlating these with biotic communities at this level may be possible, with adequate knowledge, but the result will be very diffuse. At low to moderate elevations the presence of exotic species complicates the situation enormously.

Our best suggestion is that below the association level, the difficulties be recognized, and local ad hoc arrangements and patterns of definable ecosystems be accepted. One example of an ad hoc classification at this level is that proposed by Gagne and Cuddihy for Hawaii (in Wagner et al. 1990 pp. 45-114). This is non-hierarchical classification at a very detailed level, indeed.

Another system, developed by the Natural Heritage Program of The Nature Conservancy of Hawaii, follows this ad hoc strategy at the fifth and sixth levels of a hierarchical system (Sam Gon, Ecologist, personal communication 1991). The Hawaii Natural Heritage system begins with a top level of "systems" (aquatic, subterranean, and terrestrial). The next level consists of six "elevation zones" (coastal, lowland, montane, subalpine, alpine, and multi-zonal), and the third level includes the three "moisture categories" (dry, mesic, and wet) defined on the basis of rainfall and drainage. The fourth level is based on "physiognomic categories" (desert, herbland, grassland, shrubland, forest, and mixed). The next two levels (community types and community subtypes) are defined by characteristic genera and species, respectively.

It will probably be felt that the suggestion of ad hoc arrangements for this level in the hierarchy is just the opposite of a classification, which is true. Some organization will probably be thought necessary. Stand types and landforms could be combined and arranged physiographically, if agreement could be reached as to what physiographic features are ecologically significant.

Another alternative is to group stand types by habitat. Habitat is an abstract concept consisting of one to many stands that are similar enough to be recognized and that are the living space for one or more conspicuous animals or plants. Of course, habitats exist for all organisms, but unless they are recognizable and definable, they can scarcely be classified in a useful way. Habitats of ecologically similar organisms (e.g., animal guilds) offer a possible basis for classification, but we have few conspicuous organisms in oceanic islands that occupy conspicuously distinctive situations. Habitats or habitat components (e.g., nesting or foraging habitats) for birds or fruit bats are possibilities. A necessity is that indicators of habitats are clear and conspicuous enough to be identifiable in the field. This limits habitat grouping to vegetation, soil, moisture or free water, or physiographic position.

Perhaps the most significant problem at the most detailed level of an ecosystem classification is a framework for the presentation of what we see at the stand level. Here is where the biodiversity is. At higher levels we merely talk about it. One cannot preserve a formation. One must preserve adequate stands within it. Therefore, our lowest level in the classification must be the stand or a group of mini-stands if these can be recognized.

Last Words on Classification Terms

For the purposes of ecosystem classification, criteria for distinguishing ecosystems requiring exacting, long-term, or detailed research should be avoided. The geographic facts of life - huge distances and the lack of easy access, and the resulting expenses - preclude the type of investigations on islands that are generally regarded as adequate for ecological science. For example, a classification that depends very heavily on soil or water chemistry (as with some of the systems we reviewed for wetlands and caves) will not work in the insular Pacific. For many of the most interesting islands, hit-and-run opportunities are the normal possibilities for exploration and investigation.

Finally, recognizability is the operating term. A theoretical classification, or many of them, can easily be constructed, but if their members cannot be described and recognized based on the descriptions, the system is no good. The boundary problem remains difficult, at whatever level we work in nature. Until we know what our lowest level (finest scale) ecosystems are and how to recognize their limits or boundaries, classification of the higher units is only an intellectual exercise.

A Selected List of References

Presented herewith is a list of references that anyone interested in ecosystem or vegetation classification on a world or Pacific island basis might find it profitable to read or scan. They are not selected to provide complete coverage of the field. Items on geographically localized areas outside the tropical Pacific are mostly omitted. Classification has been emphasized. Few items elaborating on the Braun-Blanquet system and the association concept are included. Items in English are emphasized.

Bailey, R. G. 1976. Ecoregions of the United States map. USDA Forest Service, Ogden, Utah.

Bailey, R. G. 1980. Description of the Ecoregions of the United States. USDA Miscellaneous Publication 1391, Washington, DC

Bailey, R. G. 1983. Delineation of Ecosystem Regions. Environmental Management 7:365-373.

Bailey, R. G. 1984. Testing an Ecosystem Regionalisation. Journal of Environmental Management 19:239- 248.

Bailey, R. G. 1987. Suggested Hierarchy for Multiscale Ecosystem Mapping. Landscape and Urban Planning 14:313-319.

Bailey, R. G. 1989. Ecoregions of the Continents. Environmental Conservation 16: map supplement, 1:30,000,000

Bailey, R. G. 1989. Explanatory Supplement to Ecoregions Map of the Continents. Environmental Conservation 16:307-309.

Bailey, R. G. and H. C. Hogg. 1986. A World Ecoregions Map for Resource Reporting. Environmental Conservation 13:195-202.

Beadle, N. C. W. 1951. The Misuse of Climate as an Indicator of Vegetation and Soils. Ecology 32:343-345.

Beadle, N. C. W. and A. B. Costin. 1952. Ecological Classification and Nomenclature. Proceedings of the Linnean Society NSW 77:61-82.

Beard, J. S. 1973. The Physiognomic Approach. pp 355-386 in R. H. Whittaker (ed.). Handbook of Vegetation Science. Part V. Ordination and Classification of Communities. Junk, The Hague, Netherlands.

Becking, R. W. 1957. The Zurich - Montpellier School of Phytosociology. Botanical Review 23:411-483.

Billings, W. D. 1964. Plants and the ecosystem. Wadsworth Pub. Co., Belmont, CA. 2nd ed. published in 1970 under the title: Plants, man, and the ecosystem.

Botkin, D. B. 1990. Discordant harmonies: a new ecology for the twenty-first century. Oxford University Press, NY.

Botkin, D. B. 1990. The Difference Between Nature Preserves and Strawberry Preserves. US Man and the Biosphere Bulletin 14(4):1-6.

Braun-Blanquet, J. 1932. Plant sociology: the study of plant communities. authorized English translation of Pflanzensoziologie (G. D. Fuller and H. S. Conard), McGraw-Hill, NY.

Briquet, J. 1970. Caracteres resumés des principaux groupes de formations vegetales etudies en un cours de geographie botanique. Annales Conservatoire et Jardin Botanique de Geneve 21:389-404.

Brown, D. E., C. H. Lowe, and C. P. Pase. 1980. A Digitized Systematic Classification for Ecosystems with an Illustrated Summary for the Natural Vegetation of North America. USDA Forest Service General Technical Report RM-73, Fort Collins, CO.

Burtt, D. J. 1938. The Classification of Tropical Vegetation Types. Oxford University Imperial Forestry Institute Papers 13:1-85.

Cain, S. A. 1932. Concerning Certain Phytosociological Concepts. Ecological Monographs 2:475-508.

Cain, S. A. and G. M. de O. Castro. 1959. Manual of Vegetation Analysis. Harper and Sons, NY.

Carpenter, J. R. 1936. Concepts and Criteria for the Recognition of Communities. Journal of Ecology 24:285-289.

Chapman, V. J. and C. B. Trevarthen. 1953. General Schemes of Classification in Relation to Marine Coastal Zonation. Journal of Ecology 41:198-204.

Christian, C. S. 1959. The Concept of Land Units and Land Systems. pp 74-80 in F. R. Fosberg (ed.). Special Symposium on Climate, Vegetation, and Rational Land-use in the Humid Tropics. Proceedings of Pacific Science Congress IX (Bangkok 1957) 20:1-169.

Christian, C. S. and G. A. Stewart. 1968. Methodology of Integrated Surveys. pp 233-280 in Areal Surveys and Integrated Studies: Proceedings of the Toulouse Conference. UNESCO, Paris.

Clements, F. E. 1902. A System of Nomenclature for Phytogeography. Botanische Jahrbucher fur Systematik, Pflanzengeschichte und Pflanzengeographie 31(Beibl. 70):1-20.

Clements, F. E. 1928. Plant succession and indicators. "A combined and condensed edition of 'Plant Succession' and 'Plant Indicators,' published by the Carnegie Institution of Washington in 1916 and 1920 respectively." Hafner, NY.

Clements, F. E. 1936. Nature and Structure of the Climax. Journal of Ecology 24:252-284.

Clements, F. E. and V. E. Shelford. 1939. Bio-ecology. Wiley & Sons, NY.

Cooper, W. S. 1926. The Fundamentals of Vegetational Change. Ecology 7:391-413.

Cowardin, L. M., V. Carter, F. C. Golet, E. T. LaRoe. 1985. Classification of Wetlands and Deepwater Habitats of the United States (2nd edition). USDI Fish and Wildlife Service, Washington, DC.

Curry-Lindahl, K. 1980a. Zoogeographic Subregions of the Pacific Realm as a Background for Terrestrial Ecological Reserves: Part 1, General Introduction and Northern and Western Pacific Regions. Environmental Conservation 7:67-76.

Curry-Lindahl, K. 1980b. Zoogeographic Subregions of the Pacific Realm as a Background for Terrestrial Ecological Reserves: Part 2, Central and Eastern Regions, etc. with Conclusions. Environmental Conservation 7:125-136.

Dahl, A. L. 1980. Regional Ecosystems Survey of the South Pacific Area. SPC Technical Paper 179., Noumea.

Dansereau, P. 1957. Biogeography, an Ecological Perspective. Ronald Press Co., NY.

Dansereau, P. 1958. A Universal System for Recording Vegetation. Contributions of the Institute of Botany, University of Montreal 72:1-58.

Dasmann, R. F. 1973. A System for Defining and Classifying Natural Regions for Purposes of Conservation. IUCN Occasional Paper 7., Morges.

Dasmann, R. F. 1974. Biotic Provinces of the World. IUCN Occasional Paper 9., Morges.

Daubenmire, R. 1938. Merriam's Life Zones of North America. Quarterly Review of Biology 13:327-332.

Daubenmire, R. 1978. Plant Geography with Special Reference to North America. Academic Press, NY.

Dice, L. R. 1952. Natural Communities. University of Michigan Press, Ann Arbor, MI.

Du Rietz, J. E. 1940. The Fundamental Units of Vegetation. Proceedings, International Plant Science Congress (Ithaca) 1:621-627.

Eiten, G. 1968. Vegetation Forms: A Classification of Stands of Vegetation Based on Structure, Growth Form of the Components, and Vegetation Periodicity. Boletim do Instituto de Botanica 4. Sao Paulo, Brazil.

Egler, F. E. 1942. Vegetation as an Object of Study. Philosophy of Science 9:242-260.

Egler, F. E. 1954. Philosophical and Practical Considerations of the Braun-Blanquet System of Phytosociology. Castanea 19;45-60.

Ellenberg, H. 1973. Die Die Ökosysteme der Erde: Versuch einer Klassifikation der Ökosysteme nach funktionalen Gesichtspunkten. pp 235-265 in H. Ellenberg (ed.). Ökosystemforschung. Springer-Verlag, Berlin.

Engler, A. and O. Drude (eds.) 1902. Die Vegetation der Erde. Leipzig.

Evans, F. C. 1956. Ecosystem as the Basic Unit in Ecology. Science 123:1127-1128.

Ford, D. C. and P. W. Williams. 1989. Karst Geomorphology and Hydrology. Unwin Hyman, London.

Fosberg, F. R. 1957a. The Vegetation Provinces of the Pacific. Proceedings of Pacific Science Congress VIII (Quezon City 1953) 4:15-23.

Fosberg, F. R. 1957b. Vegetation of the Oceanic Province of the Pacific. Proceedings of Pacific Science Congress VIII (Quezon City 1953) 4:48-55.

Fosberg, F. R. 1961a. On the Possibility of a Rational General Classification of Humid Tropical Vegetation. pp 34-59 in UNESCO. Proceedings, Symposium on Humid Tropics Vegetation (Tjiawi, Indonesia 1958). Paris.

Fosberg, F. R. 1961b. A Qualitative Description of the Coral Atoll Ecosystem. Atoll Research Bulletin 81. 11 pp.

Fosberg, F. R. 1961c. A Classification of Vegetation for General Purposes. Tropical Ecology 2:1-32.

Fosberg, F. R. 1963. The Island Ecosystem. pp 1-6 in F. R. Fosberg (ed.) Man's Place in the Island Ecosystem, Proceedings of a Symposium, Pacific Science Congress X (Honolulu 1961). B. P. Bishop Museum, Honolulu.

Fosberg, F. R. 1967. A Classification of Vegetation for General Purposes. pp 73-120 in G. F. Peterkin (ed.). Guide to the Check Sheet for IBP Areas. Blackwell Scientific Publications, Oxford.

Fosberg, F. R. 1976. Geography, Ecology, and Biogeography. Annals of the Association of American Geographers 66:117-128.

Gagne, W. C. and L. W. Cuddihy. 1990. Vegetation. pp. 45-114 in W. L. Wagner, D. R. Herbst, and S. H. Somher (eds.). Manual of the Flowering Plants of Hawaii. Bishop Museum Press, Honolulu.

Goldsmith, F. B. 1974. An Assessment of Fosberg and Ellenberg Methods for Classifying Vegetation for Conservation Purposes. Biological Conservation 6:3-6.

Good, R. D. 1947. A Geography of Flowering Plants. Longmans, NY.

Good, R. A. 1964. A Geography of Flowering Plants (3rd ed.). Wiley and Sons, NY.

Grisebach, A. H. R. 1872. Die vegetation der erde nach ihrer klimatischen anordnung: ein abriss der vergleichenden geographie der pflanzen. W. Engelmann, Leipzig.

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, Costa Rica.

Holdridge, L. R. and J. A. Tosi, Jr. 1972. The World Life Zone Classification System and Forestry Research. Proceedings of the Seventh World Forestry Conference (Buenos Aires).

Humboldt, A. von. 1805. Essai sur la géographie des plants. Schoell et Cie, Paris.

Humboldt, A. von. 1806. Ideen zu einer Physiognomik der Gewächse. Cotta, Stuttgart.

IUCN. 1973. A Working System for Classification of World Vegetation. IUCN Occasional Paper 5., Morges.

Kendeigh, S. C. 1954. History and Evaluation of Various Concepts of Plant and Animal Communities in North America. Ecology 35:152-171.

Klugh, A. B. 1923. A Common System of Classification for Plant and Animal Ecology. Ecology 4:367-377.

Köppen, W. 1923. Die Klimate der Erde. de Gruyter, Berlin.

Köppen, W. 1936. Das Geographische System der Klimate. Volume 1, Part C. in W. Koppen and R. Geiger, Hanbuch der Klimatologie. Borntraeger, Berlin.

Krajina, V. J. 1965. Biogeoclimatic Zones and Biogeocoenoses of British Columbia. Ecology of Western North America (Department of Botany, University of British Columbia) 1:1-17.

Küchler, A. W. 1949. A Physiognomic Classification of Vegetation. Annals of the Association of American Geographers 39:201-210.

Küchler, A. W. 1967. Vegetation Mapping. Ronald Press, NY.

Küchler, A. W. 1972. On the Structure of Vegetation. Ecology 53:196-198.

Küchler, A. W. 1973. Problems in Classifying and Mapping Vegetation for Ecological Regionalization. Ecology 54:512-523.

Küchler, A. W. and I. S. Zonneveld (eds.). 1988. Vegetation Mapping. Kluwer Academic Publishers, Dordrecht, Netherlands.

MacArthur, R. H. and E. O. Wilson. 1963. An Equilibrium Theory of Insular Zoogeogrphy. Evolution 17:373-387.

MacArthur, R. H. and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Major, J. 1969. Historical Development of the Ecosystem Concept. pp 9-22 in G. M. van Dyne (ed.). The Ecosystem Concept in Natural Resources Management. Academic Press, NY.

Martin, A. C., N. Hotchkiss, F. M. Uhler, and W. S. Bourn. 1953. Classification of the Wetlands of the United States. USDI Fish and Wildlife Service, Special Scientific Report - Wildlands 20. Washington, DC.

Mayr, E. 1940. Borders and Subdivisions of the Polynesian Region Based on our Knowledge of the Distribution of Birds. Proceedings of Pacific Science Congress VI (Berkeley 1939). 4:191-195.

Merriam, C. H. 1898. Life Zones and Crop Zones of the United States. USDA Bulletin of the Division of Biological Survey 10:1-79.

Moir, W. H., J. Bunin, and R. L. Hays. 1988. A Structural Classification of Terrestrial Vegetation. unpublished photocopy from USDI Fish and Wildlife Service, Thorne Ecological Institute, Boulder, CO.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, NY.

Odum, E. P. 1945. The Concept of the Biome as Applied to the Distribution of American Birds. Wilson Bulletin 57:191-201.

Omernik, J. M. 1987. Ecoregions of the Conterminous United States. Annals of the Association of American Geographers 77:118-125 plus map supplement.

Raunkiaer, C. 1937. Plant Life Forms. Clarendon Press, Oxford.

Rotramel, G. L. 1973. The Development and Application of the Area Concept in Biogeography. Systematic Zoology 22:227-232.

Rübel, E. 1930. Pflanzengesellschaften der Erde. Bern-Belin.

Schimper, A. F. W. 1898. Pflanzengeographie auf physiologischer grundlage. trans. to English by W. R. Fisher 1903. Clarendon Press, Oxford.

Schimper, A. F. W. and F. C. von Faber. 1935. Pflanzengeographie auf physiologischer grundlage. G. Fischer, Jena.

Schmithüsen, J. 1968. Allgemeine: Vegetationsgeographie. (2nd ed.). De Gruyter, Berlin.

Shelford, V. E. 1913. Animal Communities in Temperate America. University of Chicago Press, Chicago, IL.

Shelford, V. E. 1932. The Relative Merits of the Life Zone and Biome Concepts. Wilson Bulletin 57:248-252.

Shelford, V. E. 1963. The Ecology of North America. University of Illinois Press, Urbana.

Shimwell, D. W. 1972. The Description and Classification of Vegetation. University of Washington Press, Seattle.

Sukachev, V. N. (Sukatschew, W. N.). 1945. Bioecoenology and Phytocoenology. Comptes Rendus - Doklady - de l'Academie des Sciences de l'USSR 47:429-431.

Sweeting, M. M. 1973. Karst Landforms. Columbia University Press, NY.

Takhtajan, A. 1986. Floristic Regions of the World. University of California Press, Berkeley.

Tansley, A. D. 1935. The Use and Abuse of Vegetational Concepts and Terms. Ecology 16:284-307.

Thornthwaite, C. W. 1933. The Climates of the Earth. Geographical Review 23:433-440.

Udvardy, M. D. F. 1975. A Classification of the Biogeographical Provinces of the World. IUCN Occaisional Paper 8., Gland.

Udvardy, M. D. F. (discussion by L. L. Short, N. Eldridge). 1981. The Riddle of Dispersal: Dispersal Theories and How They Affect Vicariance Biogeography. pp 6-39 in G. Nelson and D. E. Rosen. (eds.). Vicariance Biogeography: A Critique (proceedings of a symposium, American Museum of Natural History, 1979). Columbia University Press, NY.

Udvardy, M. D. F. 1984. A Biogeographical Classification System for Terrestrial Environments. pp 34-38 in J. A. McNeely and K. R. Miller (eds.). National Parks, Conservation, and Development: The Role of Protected Areas in Sustaining Society. Proceedings of the World Congress on National Parks, Bali, Indonesia, 11-22 October 1982. Smithsonian Institution Press, Washington, D. C.

Udvardy, M. D. F., S. Brand, and T. Oberlander. 1978. World Biogeographical Provinces (3rd ed.) map. Whole Earth Access, Berkeley, CA.

UNESCO. 1969. A Framework for a Classification of World Vegetation. UNESCO Report SC/WS/269. UNESCO, Paris.

UNESCO. 1973. International Classification and Mapping of Vegetation. Ecology and Conservation 6. UNESCO, Paris.

Villar, E. H. del. 1929. Geobotanica. Barcelona and Buenas Aires.

von Bertalanffy, L. 1951. General System Theory: A New Approach to the Unity of Science. British Journal for the Philosophy of Science 1:134-165.

Whittaker, R. H. 1962. The Classification of Natural Communities. The Botanical Review 28:1-160.

Whittaker, R. H. 1975. Communities and Ecosystems (2nd ed.). Macmillan, NY.

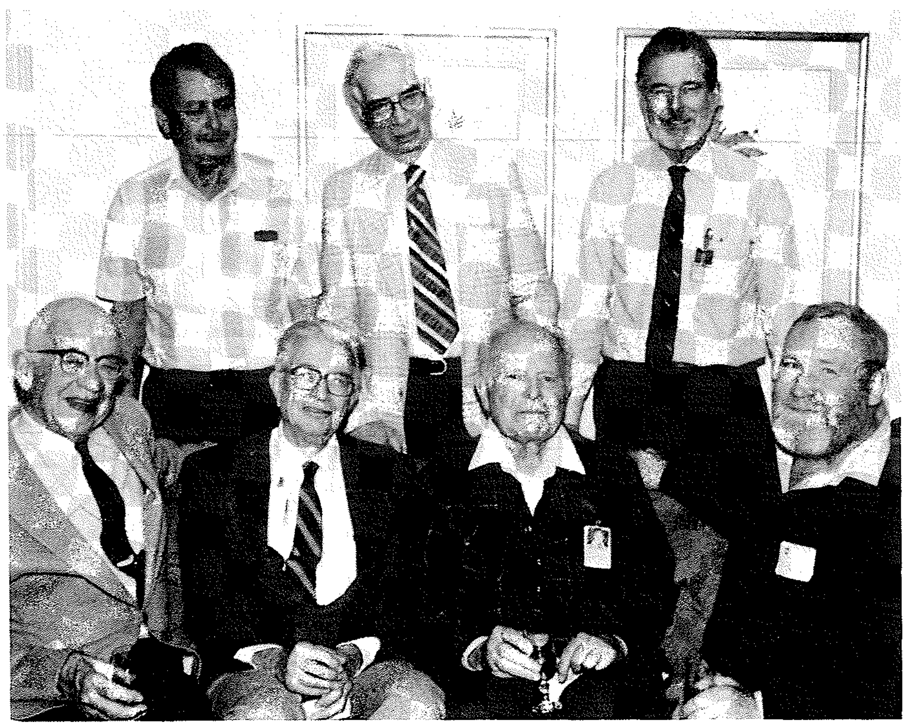
Zoltai, S. C., F. C. Pollett, J. K. Jeglum, and G. D. Adams. 1975. Developing a Wetland Classification for Canada. pp 497-511 in B. Bernier and C. H, Winget (eds.). Proceedings Fourth North American Forest Soils Conference. Laval University Press, Quebec.

NEWS AND COMMENTS

40th Anniversary Reception

On November 24, 1992, the National Museum of Natural History celebrated the 40th anniversary of the Atoll Research Bulletin. A reception was held in the Director's Office to mark the occasion and to honor F. Raymond Fosberg, who launched the journal on September 10, 1951.

Since then, the Bulletin has put out 84 volumes containing more than 600 contributions. The Bulletin has also gained widespread recognition as a primary source of information on the biota, ecology, and geology of reefs and reef islands in the world's tropical oceans.



Director of NMNH, Frank Talbot joins Ray Fosberg with a group of his old colleagues. (Back Row L to R) Royce Oliver, Myron Winestein, Frank Talbot, and (Front Row L to R) Frank Whitmore, Josh Tracey, Ray Fosberg, and David Stoddart. (photo by Jane Beck)

Dr. Fosberg is a world authority on the botany and ecology of tropical islands, whose own publications have topped the 600 mark. Although he has been officially retired for thirteen years, he continues to conduct field research and to publish the results of his studies.

Each of the sixty guests at this gathering was asked to sign a copy of the 40th anniversary issue of the Atoll Research Bulletin, which was presented to Dr. Fosberg as a keepsake.

Josh Tracey, a contributor to the first issue of ARB, signs the 40th Anniversary issue as Ian Macintyre looks on. (photo by Jane Beck)

Frank Talbot presents Ray Fosberg with a signed copy of the 40th Anniversary issue of ARB. (photo by Jane Beck)

Book Notice

THE TURF ALGAL FLORA OF THE GREAT BARRIER REEF. PART I. RHODOPHYTA. Ian R. Price and Fiona J. Scott. James Cook University, Townsville, 1992. xii + 266 pp. (including 81 figs). Softcover.

Available from: The Bookshop, James Cook University, Townsville, Qld 4811, Australia [Phone (077) 814 812, Fax. (077) 251 209]. Price AUS$61.95 (by surface mail within Australia or overseas). Cheques should be made payable to "James Cook University Bookshop". For credit card payment please specify whether Bankcard, MasterCard or Visa, give card number, expiry date and name of card-holder, and include your signature.

This volume deals with the turf-forming species of red algae occurring on the Great Barrier Reef. The publication provides detailed descriptions and illustrations of the 74 species recorded, with emphasis on vegetative features. In addition, data on nomenclature, type material, voucher specimens, habitat, seasonality and geographical distribution are given. Genus descriptions, keys to genera and species, a glossary and taxonomic index are also included. This is the first detailed treatment of the taxonomy and distribution of the turf algae which occur on coral reefs, where they are of major importance in trophodynamics. Although written for Australia's Great Barrier Reef, the work should prove useful throughout the tropical Indo-Pacific region.

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