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ABSTRACT

This is the first paper in a two-part series describing the patterns of inquiry used in ecology. Ecological knowledge and research are analyzed in terms of two sets of concepts: ecological problem areas, and principles of biological inquiry. Problem areas identified are classification and taxonomy, energetics, nutrition and metabolism, genecology, and distribution. It is argued, using illustrations from the ecological literature, that different problem areas require different data and exhibit different methods and techniques. Four principles of biological inquiry are identified: the principle of antecedent-consequent, the principle of structure-function, the principle of homeostasis, and the principle of regulation. The effects of different principles on the modes of inquiry within a problem area are illustrated by comparing ecological research which focuses on the individual as the unit (an application of the principle of antecedent-consequent) with research that treats the community as a unit (using the principle of structure-function). (EB)

Patterns of Enquiry in Ecology: I. Principles of Biological Enquiry and Problems of Ecological Enquiry.[1]

F. Michael Connelly

THE PROBLEM: ITS TERMS AND LIMITS

Ecology is a science with few established theories and concepts and with many seemingly competitive ideas. For the most part enquiry proceeds along independent lines without serious debate but, periodically, confrontations occur and debate flourishes. There are, for instance, issues of forest classification; of the character of vegetation distribution; of the role of dominant species in community maintenance; of the conceptual status of the term "community;" of the proper object of ecological research; and of population control factors. Whether or not apparent differences are raised to the level of debate it is often difficult to make sense of the adherents of one line of enquiry from anothers vantage point. At first inspection debates often seem unresolvable by further empirical research and arguments appear as if different authors were using different languages to investigate the same problem and as if each were unable to understand the language of the other. We may, for instance, imagine two protagonists debating whether a lake is an unique whole or an open system.

The overriding intention of this paper is to make sense of diversity in ecological enquiry by raising differences to the level of opinion.

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1. This paper is based on a dissertation recently completed at the University of Chicago.

Differences so seen become matters of assumption, starting point, or initiating conception in enquiry. Such an understanding of diversity provides a framework for seeing the merits of diverse enquiries and may, thereby, contribute to debate. Accordingly, the study on which this paper is based began with a search for the principles which serve as starting points for ecological enquiry.

Principles of enquiry are the concepts in which any given enquiry has its origin as, for example, the concepts of structure and function in biology. According to Schwab, principles function in enquiry by providing the terms in which problems are formulated; by dictating the data required and, therefore, delimiting the procedures necessary to obtain the data; and finally, by providing the terms in which data are interpreted and new knowledge formulated.[2]

Principles exist as a more or less coherent set of terms embedded in the literature; in its problems, its methods, its conclusions, its reviews, and its resource texts. Accordingly, this study is based on an analysis of several hundred papers published in the journals of plant and animal ecology. The analysis was restricted to English speaking journals and, for the most part, to literature published since 1900.

The analysis in terms of principles of enquiry uses two sets of concepts - Ecological Problem Area and Principle of Biological Enquiry - for organizing the literature. The problem areas are our way of classifying the variety of particular problem with which every enquiry begins. Different problem areas use different terms for analysing the subject-matter into parts. Thus, one problem uses the term "ecotype" and another problem uses the term "trophic level." Accordingly, in the search for principles, these are the most visible terms and they allow us to establish a continuity from paper to paper.

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2. Joseph J. Schwab, "What do Scientists do?", Behavioral Science, V (1960), 1-27

The principles of biology are the classes of principle used in the biological sciences and, of course, represent different kinds of treatment of the parts. In the framing of a problem, therefore, we are able to distinguish between the parts and their treatment in enquiry. Accordingly, in the search for principles, the principle of biology used by any enquiry gives the form taken by the ecological principle. The combination of the terms of the two sets of organizing concepts gives us the principles and patterns of ecological enquiry.

The paper is divided into two parts - Principles of Biological Enquiry and Problems of Ecological Enquiry <u>and</u> Principles and Patterns of Ecological Enquiry - of which this is the first.

ECOLOGICAL PROBLEM AREAS

The problem area is our most patent organizer since it is here that terms representative of the principles are clearly visible. Accordingly, our first sorting of the literature is conducted in terms of the problem areas. On this basis we find that ecology is divisible into five areas, classification and taxonomy, energetics, nutrition and metabolism, genecology and distribution. Let us define each problem area by specifying the problems appropriate to each.

Classification and Taxonomy

The problem of ecological classification and taxonomy is the problem of constructing classes for the <u>complexes</u> of organisms occurring together on the landscape. Due, perhaps, to the immobility of plants this problem area is more actively pursued by plant ecologists than by animal ecologists.

Among the major subproblems of ecological classification and taxonomy are the following:

1. Selection of index criteria by which to establish classes. The various classification schemes use index criteria ranging from characteristics of the organisms, to characteristics of the environment, to combinations of both, and include both structural features, such as physiognomy, and functional features, such as the production to respiration ratio.

2. Determination of the repeatability of ecological units on different parts of the landscape. This problem is closely related to problem 3.

3. Determining whether organisms are distributed discretely or continuously on the landscape.

While ecologists have tried to solve problems 1 and 2 as if they were matters of fact--by arguing from one or another set of data--the problems are resolvable solely as matters of principle, since this is the only basis on which to select the relevant facts. Furthermore, since different men use different principles the choice of principle remains a problem.

4. Grouping classes into hierarchical systems. Both phylogenetic and nonphylogenetic systems are found in the literature.

Energetics

The problem of energetics is the problem of determining energy status and energy change, especially of transformations of potential energy in chemical form, for ecological systems and their parts. This problem receives attention from both practical and theoretical sides. On the practical side ecologists are concerned with land use and comparative crop production, including such crops as hardwood forests. The term "production ecology" is commonly applied to this side of energetics. On the theoretical side many ecologists advance the idea that a comprehensive theory of ecology must be based on energetics. In the present state of the field, however, comprehensive theories have advanced so little that most of what they might at some future date comprehend is now distributed among the other four of our five problem areas. Among the major subproblems of energetics are the following:

1. Determination of the biomass for ecological systems as a whole and determination of the distribution of biomass within systems. Since, as we later show, there are different ways of conceiving system parts there are correspondingly different biomass distributions.

2. Determination of paths of energy flow to, through and out of ecological systems. There are, of course, different conceivable pathways depending on the parts employed by the principle in question.

3. Determination of energy balance and energy efficiencies for systems as a whole and for their various parts. In addition to the multiplicity introduced by there being different conceivable parts and, therefore, different conceivable pathways there are, for a given set of parts, different kinds of calculable efficiencies.

Nutrition and Metabolism

The problem of nutrition and metabolism is the problem of determining the nutritional status and nutritional change for ecological systems and their parts. While the form of this problem is the same as that for energetics the two problem areas have different histories of enquiry. Much of the early research in ecology was in the area of nutrition and metabolism and tended to be conducted in terms of minimally complex principles. Thus we see papers of the sort, "The effect of low calcium levels or species X." Energetics, on the other hand, is a relatively recent ecological problem and tends to be guided by more complex principles.

In addition to the historical differences the two problem areas are treated in most papers as having quite different boundaries in enquiry. This can be seen by comparing the list of problems for each area. As might be expected, much nutritional enquiry takes the environment as its starting point. Conversely, very little research of the kind we are classifying under energetics takes account of the environment as other than a source of energy input to ecological systems. These differences reflect different foci in enquiry, and not differences in the proper boundaries of the two problem areas. Among the major subproblems of nutrition and metabolism are the following:

1. Determining and accounting for correlations between the location of organisms or ecological systems on the landscape and nutritional factors at those sites.

2. Determination of the nutritional requirements and tolerance range of species. As we later point out, the species is only one kind of part conceived for use in the analysis of ecological systems. However, we find few papers written in terms other than those of individuals or species.

3. Determination of pathways of nutrient flow through ecological systems including what is commonly called "biogeochemical cycles." In our enquiry we do not include the problem of determining biogeochemical cycles for the biosphere as a whole. There are, of course, reports in the literature of this sort.

Genecology

Genecology is here distinguished from classical and population genetics on the grounds of its concern for genetic relationships between groups of organisms and their environment. Classical genetics focuses on the individual and emphasizes particular traits while population genetics focuses on the organisms themselves and not on the relationship between organism and environment. In general, population genetics deals with a symbolic expression of gene frequencies in groups treated as formal entities. Genecology, on the other hand, is more concerned to identify particular groups and to take account of their distribution in time and space. This concern points to one of the inadequacies of our classification scheme of problems since genecology might well be classified as a subhead of classification and taxonomy. However, since many studies are concerned with establishing taxonomy as a ground for other research while another group of studies are concerned with phylogenetic problems in their own right, we retain the distinction and include the latter under genecology.

In general, studies in genecology as we have defined it deal with single species. Only a small number of studies attempt to analyze the genecological structure of communities of species. Among the major subproblems of genecology are the following:

1. Determination of infraspecific phenotypic variation on the landscape and determination of the degree to which this variation is due to phenotypic plasticity of given genotypes and the degree to which it is due to different genotypes.

2. Determination of the distribution of genotypes with respect to variations in the environment.

3. Determining whether the genetic units (ecotypes) vary continuously or discretely on the landscape. This problem is formally similar to the third problem of classification and taxonomy.

4. Determination of the genetic relationships among ecotypes.

5. Determination of the processes and mechanisms by which ecotypic variants arise given variable environments and common gene sources.

Distribution

The problem of distribution is that of developing accounts of the kinds, numbers and distribution of organisms on the landscape. Among the major subproblems of distribution are the following;

1. Determination of population growth patterns and age structures under varying environmental conditions, including other organisms.

2. Determination of the controls of population growth patterns.

3. Developing biotic and environmental accounts of the temporal distribution of kinds and numbers of organisms.

4. Developing biotic and environmental accounts of the spatial relationships among organisms of a single species and between organisms of different species.

Since problems stem from principles, and incorporate the principles in the terms of the problem, they radically affect the way in which a subject-matter common to them all is viewed. For example, in classification and taxonomy, climax types, pattern and fidelity are some of the terms brought to bear on the subject-matter. For energetics, on the other hand, trophic level, food chain, food pyramid, and pyramid of numbers are the operative terms. In nutrition and metabolism, biogeochemical cycle, tolerance, and nutritional requirement are, of course, a few of the terms of reference. For genecology, familiar terms include ecotype, selection, migration, and gene frequency and, for distribution we obviously speak of population, growth rate, density and distribution.

The effect of these terms on the subject-matter of enquiry is easily seen in the way each set of terms discriminates a different set of parts in the common subject-matter. To illustrate, in classification and taxonomy, individuals, species, synusia, and homogeneous association are some of the significant parts discriminated. In energetics, trophic levels, links in a food chain, producer, consumer, and decomposer may, each in its place be called upon to serve the role of part. For nutrition and metabolism, individuals and nutrients, parts of individuals such as roots, trunk, leaves and, where studies parallel those in energetics, trophic levels, may each serve as parts. In genecology, species and ecotypes serve as parts and, in distribution, individuals, species or two or more species treated as a unit, may play the role of part.

Patterns of Enquiry According to Problem Area

We have seen that the problem areas consist of a number of different kinds of parts. This means that the problem areas are, at least partially, specified by their parts and the principles that determine them. Furthermore, it means that the problem areas, to a certain degree, require different data and exhibit different methods and techniques. As an example let us contrast certain cases in distribution with others in genecology. (We shall take as given the role of principles in determining the initial choice of what landscape is worth sampling, the choice of its boundaries, and whether it is to be treated as an interacting system or merely as a spurious assortment of species.)

In the problem of distribution it is necessary to obtain data with respect to kinds and frenquency of species present, their spatial relationships to one another and to the environment, and the extent of their distribution. One method of obtaining these data is by quadrats sampling of the landscape. (Quadrats are defined, localized spaces on the landscape.) Organisms falling within the quadrat are classified, counted and their positions noted. A paper by Ramsey and Deleeuw[3] will illustrate our point. In our excerpt from it we see the problem of the paper and the resultant use of quadrats; the counting and identification of included species; and an explanation of why their sampling method is random. The problem is set forth as follows:

> The value of vegetation recording in soil-survey operations in Northern Nigeria has long been recognized, and the making of routine vegetation records along soil survey traverses has been a feature of reconnaissance soil surveying in this region. . . . Since 1957/58 the Soil Survey of Northern Nigeria has been carrying out a reconnaissance survey of the Middle Gonbola valley. . . .[4]

Their methods are described as follows:

> Because of a limited time and access route random sampling over the whole area could not be undertaken. On areal photographs at scale 1:30,000 the different soil associations were identified and demarkated and within each such unit sampling of the different vegetation patterns was undertaken. It was laid down that every pattern should be sampled and that the sample areas should be as representative as possible of a homogeneous site class. . . . Plots (quadrats) were laid out in the form of a rectangle 110 x 22 yd. (100.5-20 m), using ranging poles for demarkation, an optical square for right angles and a measuring wheel for distances. All arboreal vegetation was recorded by diameter class, each species separately. . . . For each plot the number of individuals of each species was totalled. . .[5]

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3. D.M. Ramsey and P.N. Deleeuw, "An Analysis of Nigerian Savanna: I. The Survey Area and the Vegetation Developed over Bima Sandstone," Journal of Ecology, LII (1964), 233-54.

4. Ibid., p. 239. 5. Ibid., pp. 233-34.

In genecology, which also contains a problem of identification, the ecologist must determine whether two populations do, in fact, represent two ecotypes. It may be that phenotypic differences merely reflect phenotypic plasticity. In order to obtain data, reciprocal transplantation of representative members of the two populations is required. By comparison of transplant phenotypes with their new neighbors and with their parent populations, differences in the two populations may be attributed to the plastic expression of a single genotype subjected to variable circumstances. In either case the initial problem is settled, and by markedly different methods from those outlined for classification.

We see the method of reciprocal transplant in genecology illustrated in a paper by McMillan. He states his problem and demonstrates the necessity of the method in the following:

> The grassland community is an ideal experimental unit. . . . In two previous studies of the fundamental ecological unit, transplanting of members to a uniform garden proved helpful in understanding behavior within grassland communities. . . . A community from the loess hills . . . was selected for comparison with one in the sand hills. . . . The two communities' sites have obvious soil and climatic differences. However, they contain a surprisingly similar list of species. . . . In the present evaluation, the separation of habitat effects from genetic controls within the community is approached by the reciprocal transplanting of members. . . .[6]

The reciprocal transplant method is now described:

> Ten clones of each of the nine taxa were removed from the Lincoln community site. . . . Each clone was divided and tagged so the two pieces could be placed in a uniform garden at Lincoln and two pieces could be taken to a uniform garden at Halsey. . . . At Halsey clones were collected and divided in a uniform fashion similar to that used at Lincoln. Following the planting of Halsey material, tagged clonal pieces were taken to Lincoln for garden and greenhouse studies.[7]

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6. C. McMillan, "Nature of the Plant Community: III. Flowering Behavior Within Two Grassland Communities Under Reciprocal Transplanting," American Journal of Botany, XLIV (1957), p. 144.

7. Ibid., p. 145.

An adequate account of the relationship between terms and methods requires an examination of commonalities, as well as differences, between problem areas. Where a principle is employed in more than one problem area and there are, therefore, shared terms, certain methods and techniques are also the same for the two areas. This is exhibited between the two problems of energetics and metabolism, where the enquiry is aimed at obtaining correlative information on matter and energy. For example, an energeticist may ask at what rates and quantities energy flows through a system and at what points it is trapped, and passed on. Similarly, an enquirer interested in the metabolism of the system may ask the same questions with respect to nutrients.

This is well illustrated in four of Ovington's papers dealing with the same subject-matter; the same plantation of forest trees. The two problems of energetics and nutrition are clearly enough seen in the titles of the papers: "Mineral Content in Plantations of Pinus sylvestris L.";[8] "The Circulation of Minerals in Plantations of Pinus sylvestris L.";[9] "Dry Matter Production by Pinus sylvestris L.";[10] and, "Some Asoects of Energy Flow in Plantations of Pinus sylvestris L."[11]

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8. J.D. Ovington, "Mineral Content in Plantations of Pinus sylvestris L.," Annals of Botany, XXIII (1959), 75-88.

9. J.D. Ovington, "The Circulation of Minerals in Plantations of Pinus sylvestris L.," ibid., XXIII (1959), 229-39.

10. J.D. Ovington, "Dry Matter Production by Pinus sylvestris L.," ibid., XXI (1957), 287-314.

11. J.D. Ovington, "Some Aspects of Energy Flow in Plantations of Pinus sylvestris L.," ibid., XXV (1961), 12-20.

The method followed in all these papers is to mark out a sample plot within each of thirteen plantations of pine. Within the plot 100 trees are randomly selected and measured for bole and canopy characteristics. One of these trees, taken as representative of the plot and of the plantation as a whole, is selected and cut down. Dry matter and mineral determinations are made for the tree as a whole and for its various parts.

The Ovington papers are particularly useful to us since they exhibit a case where the same principle is employed in both problems, with the result that virtually the same data serve two problems areas. In some cases single papers treat two problem areas and, of course, employ a single principle. As seen from the title, Ovington and Madgwick's paper, "Distribution of Organic Matter and Plant Nutrients in a Plantation of Scots Pine," [12] is a case in point.

Notwithstanding the above mentioned similarities between problem areas (and there are others) a review of the literature reveals that differences between the areas, and not their similarities, stand out most clearly. The differences between problem areas with respect to terms and, consequently, methods and techniques are, of course, reflected in formulations of ecological knowledge. To the extent that differences exist there is an exclusiveness of knowledge formulated in terms of each problem area. Contrast, for example, an energetic account of an ecological system in terms of energy fixation, efficiency of energy translocation, and fixed biomass at certain trophic points; with a genecologist's account of an ecosystem in terms of a number of ecotypes at equilibrium with one another and their habitats, and with a fixed rate of genic exchange.

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12. J.D. Ovington and H. A. I. Madgwick, "Distribution of Organic Matter and Plant Nutrients in a Plantation of Scots Pine," Forest Science, V (1959), 344-55.

Both accounts contribute something special to the understanding of the same subject matter, for example, a flood plain forest. Such a forest, taken along a time continuum, may, by an energeticist, be rated according to its primary productivity versus its losses due to respiration and decay. In succession from the young to the old parts of the system the relative value of production with respect to respiration decreases until at the older stages they are approximately equal. This situation defines the mature system, the climax. The net productivity of the system (rated as biomass), of course, increases along the continuum.

A genecologist, looking at the same system accounts for the vegetation by showing that the time continuum corresponds to a wet-dry soil continuum. As one progresses along the continuum the relative adaptive value of the various ecotypes change. Some values decrease while others increase. Consequently, ecotypes enter the system with low adaptation. As the soil dries adaptation increases, reaches a maximum, and eventually decreases as conditions become to dry for maximum reproducibility. At the oldest successional stages all ecotypes are about equally adapted and there is little change in ecotypic composition of the forest. This situation defines the climax. Thus, succession and climax are accounted for by changing relations between production and respiration in the one case and by changing ecotypic adaptation in the other case.

PRINCIPLES OF BIOLOGICAL ENQUIRY

The major purpose of this section is to set forth the principles of biology as described generally by Schwab[13] and to show how they are

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13. Joseph J. Schwab, personal communication; Joseph J. Schwab, "Invitations to Enquiry," in Biology Teachers Handbook (New York: John Wiley and Sons, Inc., 1964), pp. 45-226.

reflected in ecological research. The principles of biology are, antecedent-consequent, structure-function, homeostasis and regulation. We will describe the general characteristics of each principle, give examples from physiology and ecology, and indicate the sources of systematic error in the use of each principle.

The Principle of Antecedent-Consequent

According to this principle the organism is treated as a collection of antecedent-consequent events. This is seen in Mill's, A System of Logic.[14] Research focuses on some relevant element (organ, species, trophic level) and treats it in terms of its immediate and long term antecedences and consequences. Schwab notes that this is an oversimplification recognized by Mill. Mill writes:

> All organized bodies are composed of parts similar to those composing inorganic nature, and which have even themselves existed in an inorganic state, but the phenomena of life, which result from the juxtaposition of those parts in a certain manner, bear no analogy to any of the effects which would be produced by the action of the component substances considered as mere physical agents. To whatever degree we might imagine our knowledge of the properties of the several ingredients of a living body to the extended and perfected, it is certain that no mere summing up of the separate actions of these elements will ever amount to the action of the living body itself.[15]

The advantage of this principle is that it allows research to begin amidst an otherwise incomprehensible complexity. Where appropriate (i.e., in cases other than those pointed to in the quotation from Mill), the results of such research may subsequently be combined by monography to give a more adequate account of the subject-matter.

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14. John Stuart Mill, A System of Logic, Ratiocinative and Inductive, Being a Connected View of the Principles of Evidence and the Method of Scientific Investigation (London: Longmans, Green and Company, 1930).

15. Mill, A System of Logic, cited by Joseph J. Schwab, Philosophical Aspects of Biology: The Decision Points of Biological Enquiry (Chicago: University of Chicago Press, 1960), p.4.

The antecedent-consequent principle permits the use of a number of research methods described by Mill. Three of the most commonly used methods in biology are the "method of difference," the "method of similarity" and the "method of concomitant variations." The element in question is modified or removed and the resulting modification or disappearance of an action is inferred to be the consequent of the manipulated element. An attempt to discriminate a possible antecedent for myxedema by the use of the method of difference is seen in the following:

> . . . I have produced the condition of myxedema by simply excising . . . the thyroid gland of the monkey.[16]

An illustrative case in ecology is provided by Oosting and Billings in their paper, "Factors Affecting Vegetational Zonation on Coastal Dunes."[17] In their attempt to account for the differential distribution of three dune plants the authors first use the method of concomitant variations. They lay out transects and find that the distribution pattern is not accountable in terms of soil conditions or temperature. They then turn to water conditions and use the method of differences. Here, under controlled conditions for soil factors and for temperature plants are grown under five water treatments; no treatment, water daily, water alternate days, seawater daily, and seawater spray daily. They compare the growth of each species under experimental and field conditions. Two of the species react differently to the fifth water treatment leading the

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16. Victor Horsley, "On the Function of the Thyroid Gland," Proceedings of the Royal Society of London, XXXVIII (1885), v, cited by Schwab, Philosophical Aspects of Biology, p. 16.

17. Henry J. Oosting and W. Dwight Billings, "Factors Affecting Vegetational Zonation on Coastal Dunes," Ecology, XXIII (1942), 131-42.

authors to infer that:

> . . .the relative tolerance of the two species to salt spray is such that Andropogan dies under exposures which scarcely affect Uniola. Apparently, the general distribution of the two species on the dunes is largely controlled by the extent of exposure of the habitat to wind born spray. . . .[18]

According to Schwab the research patterns arising from any principle of enquiry has its own source of systematic error. In the case of the antecedent-consequent pattern the error grows out of the fact that there is no criterion for identifying the unit under investigation as the appropriate one i.e., capable of being treated as a single event having a single consequent and a single antecedent. In the case of the myxedema research, for example, both the parathyroid glands and the thyroid gland were removed and a set of consequences were obtained which are not part of the myxedema syndrome.

The Principle of Structure-Function

Schwab gives the following account of the principle of structure-function:

> In this conception the "whole" has its place. It is a "going" concern with a certain character or nature. That character or nature is expressed through a number of capacities and activities characteristic of it. Thus the character or nature we call "animal" is expressed through a catalogue of capacities and activities as familiar as it is venerable, that is, ingestion, digestion, distribution and assimilation, excretion, locomotion, integration, reproduction, and so on.

> . . . These capacities and activities, in turn, make certain demands. There are conditions that must be held within bounds and needs that must be supplied if they are to be maintained. It is here that the "parts" play their role. They are servants of the whole, supplying its needs as well as constituting its visible existence. . . . Organs, in turn, may be treated as wholes while we investigate, as their parts, the tissues, the variety of cells, even the microstructures, which compose and maintain them. . . . The leading question we are to ask in each such investigation is clear enough. What is the role of each part in the whole economy? It is at this point that the conception makes it crucial commitment, sets forth the notion which is at once its greatest strength and its sorest point. That notion is briefly and simply this: The <u>structure</u> of every part, the <u>location</u> of every part, and its observable <u>actions</u> of or in every part are all appropriate

18. <u>Ibid</u>., p. 141.

to, neatly fitting for, the role it plays in the whole.[19]

Schwab lists seven kinds of evidence for function which are clearly derived from the character of the principle. The seven are:

1. The overall shape and appearance of an organ or part
2. The observable change or motion of that part
3. The relation of that part to other parts
4. The shape and appearance of that organ's <u>components</u>
5. The observable change or motion of the <u>components</u>
6. The relation of the <u>components</u> to one another
7. The behavior of the organism[20]

An example of this form of enquiry in ecology is seen in Engelman's paper, "The Role of Soil Arthropods in the Energetics of an Old-Field Community."[21] For Engelman, community organization is a matter of trophic levels and their relations to one another. Different species have different functions in maintaining the energy structure of the community and one of Engelman's problems is "to indicate their (oribatid mites) role in the soil industry."[22] To do this he takes soil samples and uses radioisotope tracers to obtain data on biomass, population number and food habits. From these data he concludes that:

> The main role of the soil herbivores was found to be that of controlling the fungal and bacterial populations which are breaking down the dead materials. The arthropods can both accelerate and retard the growth of the decay organisms.[23] The soil carnivores serve as population controls on the herbivores.

There are three sources of systematic error in structure-function

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19. Schwab, <u>Biology Teachers Handbook</u>, pp. 188-90.

20. <u>Ibid</u>., p. 179.

21. Manfred D. Engelman, "The Role of Soil Arthropods in the Energetics of an Old-Field Community," <u>Ecological Monographs</u>, XXXI (1961), 221-38.

22. <u>Ibid</u>., p.222.

23. <u>Ibid</u>., p.237.

research. First, while it is usually clear in physiology that the relevant whole under examination is the organism this clarity of boundary does not always exist. In ecology boundaries are often extremely vague and must be carefully specified in each research. Second, while research tends to proceed as if a given part had a single function it is often the case that the part has several functions depending on how the part is discriminated and on the kind of function looked for. Thus, in our arthropod case, the herbivores function in maintaining appropriate microbial numbers and in maintaining a balance between living and decaying organic matter. Third, there is no sure rule for determining which of the changes taking place in or in the neighborhood of a part are the ones to be treated as effecting the function. The problem is compounded in ecological research since the organisms are doing so many things. For example, the chewing and grinding may not have any long range effect on microbial decomposition rates as inferred by Engelman.

The Principle of Homeostasis

According to this principle the biological subject-matter is organism-as-part-of-entire world. "Organism" is distinguishable from "environment" only by virtue of its maintained inhomogeneity with the remainder of the object. The mechanisms by which this individuality is maintained are called "homeostases."

The aims of research are, first, to discover what materials, substances, conditions or constituents are homeostatically maintained in a state of relative balance and, second, to discover the mechanisms for maintaining these homeostases. Accordingly, the research treats pairs of elements as reacting to one another. Research concerned with discovering mechanisms proceeds by modifying one element and by recording changes in the second element. Claude Bernard's study of the control of blood sugar levels is a physiological case in point.[24] Bernard first establishes the relative constancy of blood sugar level in dogs by varying their starch intake. Next, under conditions of no starch intake he attempts to trace the control of the sugar content of blood by determining the sugar level in blood entering and leaving a number of organs. From these data he discovers that the liver acts as an agent of compensatory withdrawal through storage and as an agent of compensatory replacement through release of the stored sugar.

A comparable ecological example is seen in Huffaker's paper "Experimental Studies of Predation: Dispersion Factors and Predator-Prey Oscillations."[25] Huffaker begins by questioning the prevailing conception that predator-prey systems are extinguished without a prey input source. He sets up a series of predator-prey situations with two species of mites in an attempt to generate a stable system. He records and plots the densities against time for both species for each situation. In this case the aim of the research is not that of Bernard's i.e., to identify a homeostatic mechanism existing in an actual situation, rather, the attempt is to demonstrate the possibility of a homeostatic situation arising out of some organization of a predator-prey situation. Nevertheless, the guiding conception of the research is homeostasis.

Huffaker is not entirely successful in creating a balanced predator-prey system but he does identify some of the mechanisms required by such a system. For example, he writes that:

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24. Claude Bernard, An Introduction to Experimental Medicine, trans. by Henry Copley Greene (New York: McMillian Co., 1927).

25. C.B. Huffaker, "Experimental Studies of Predation: Dispersion Factors and Predator-Prey Oscillations," Hilgardia, XXVII (1958), 343-83.

> . . . for a perpetuating system sufficient potentialities must be incorporated to assure several or many such arenas of "last survivors." This system would leave little probability that all such "last survivors" will simultaneously starve and some find new areas inhabited by the prey.[26]

Prey input is conceived by Huffaker to be part of the homeostasis. Thus he writes:

> That self-sustaining predator-prey coactions cannot be maintained without "migration" is self evident. In this type of study the distinction between migration and any movement at all becomes ephemeral. The author disagrees that these migrations must be from beyond the limits of a reasonably adequate system. They may be a result of normal movements within the system--if the system is adequate to give expression to the inherent balance in the biological relations of the predator, its prey, and their coinhabited environment.[27]

One of the error sources in research conducted according to the conception of homeostasis lies in the fact that two or more controlled factors may be mutually or commonly controlled. This is the case for carbon dioxide pressure and oxygen pressure in the blood. As Haldane notes, "If we diminish rapidly and very considerably the pressure of oxygen in the inspired air. . . ." the two factors interact such that "the final result is a compromise, in which the breathing is only slightly increased."[28]

The Principle of Regulation

In this conception the emphasis is on the whole and its ability to use a variety of parts and processes to preserve itself. Each organism has a repertory of such parts and processes and, in consequence, each organism has several states of normality. According to this conception, when an organism is confronted by a new or changing environment or by a loss in the repertory, the organism responds by the modification of a

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26. Ibid., p. 378.

27. Ibid., p. 379.

28. J.S. Haldane, The Philosophical Basis of Biology (New York: Doubleday, Doran and Co., Inc., 1931), pp. 53-54.

part, by the development of a new part or by other parts assuming the lost service. The organism's needs may also be served in a new and different way. For example, under conditions of bodily oxygen debt energy is obtained by fermentation and not by oxidation.

The research goal is to determine the potentialities of the organism for maintaining itself and the variety of parts and functions it can generate. Accordingly, a method is used which superficially resembles the antecedent-consequent method of difference. The researcher alters, adds or removes part of the organism or stringently varies some factor of the environment. However, unlike the procedure followed in antecedent-consequent research the researcher identifies the response of as wide a variety of parts and processes as is experimentally feasible.

A physiological example of regulation is seen in Hendricks and Borthwick's review paper, "Control of Plant Growth by Light."[29] In this paper the authors describe the relationship between plant behavior and the response of the light sensitive protein "phytochrome." Phytochrome has two interconvertible forms. The conversions are reversible and are brought about in two ways, namely, by variations in the quality of the light and by the presence or absence of light. This is seen in the following sketch.

$$P_{660} \underset{730\ m\mu}{\overset{660\ m\mu}{\rightleftharpoons}} P730 \xrightarrow{Dark} P_{660}$$

The left side of this sketch represents an equilibrium reaction. The reaction, for example, is driven to the left when there is a relatively high proportion of long wave length. This occurs for lower-story plants in forests

29. S. B. Hendricks and H. A. Borthwick, "Control of Plant Growth by Light," in Environmental Control of Plant Growth, ed. by L. T. Evans (New York: Academic Press, Inc., 1962), pp. 234-63.

where shorter wave lengths are filtered out. Since P_{730} is enzymatically active, plant metabolism and, thereby, growth characteristics are modified. For the right side of the sketch the conversion is modified by temperature. This conversion is related to photoperiodic and temperature conditioning required for flowering and seed germination in some species.

An ecological example of regulation is seen in Root's study, "The Niche Exploitation Pattern of the Blue-Grey Gnatcatcher."[30] Root's problem is to determine the repertory of behavioral and habitat responses of the gnatcatcher when these birds are confronted with a seasonally variable environment. He remarks that:

> Species which occupy habitats that fluctuate widely in their suitability for existence must either remain highly generalized or possess adaptations--that permit the population to survive when its specialized requirements fail.[31]

Two types of adaptations are possible, namely:

> . . . either the populations can be morphologically variable . . . or all of the individuals may possess a similar range of capability.[32]

Root determines that the gnatcatcher uses the second, functional, means of adjustment.

The seasonal changes constitute the environmental manipulations. Root merely identifies changes in various environmental indices such as degree of leafing and gnat population densities, and correlates these measures with observed bird behavior. He concludes with the following

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30. E. Root, "The Niche Exploitation Pattern of the Blue-Grey Gnatcatcher," Ecological Monographs, XXXVII (1967), 317-50.

31. Ibid., p. 317.

32. Ibid., p. 344.

statement:

> Within each set of limits the gnatcatchers are able to alter their behaviour by responses to changes in the environment ... Thus, the gnatcatcher changed from chaparral to oak woodland habitats during the late spring, from twig to foliage insects following bud-burst, from small arthropods in the winter to larger prey in the summer and from mirids and lepidopterous larvae in March-May to Membracids and Cicadellids during June-August.[33]

In addition Root shows that the gnatcatcher has a repertory of methods of catching prey and that which method is used depends on the habits of the particular prey in greatest abundance at any time.

The systematic error in the principle of regulation is that it does not identify the normal state.

Schwab claims that the various general biological principles, with the possible exception of an antecedent-consequent conception, are distinctly different ways of getting distinctly different kinds of knowledge about the subject-matter. Consequently, one measure of the maturity of a field is the extent to which it exploits all the methods. Historically, modern science has come only recently to exploit regulation as a principle. Hence, fullest sophistication is likely to be indicated by researches using this principle. As we shall see in succeeding pages, the principles of antecedent-consequent, structure-function and homeostasis are widely used in ecology. There are few, if any, full scale studies of ecological communities in terms of regulation.

Patterns of Enquiry According to Principle

The papers in one problem area may, of course, derive from several different principles. When this occurs we see that the principle establishes limits on the kind of part required and, therefore, selects among

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33. *Ibid.*

the possible parts for any problem. In addition, the principle, as against the problem, commonly dictates the part-whole relationship in any enquiry. These roles of principles and problems are clearly seen, for example, in the ecological literature on classification and taxonomy. One principle--which we will designate as Principle A requires a minimally complex unit such as the individual and is an application of the principle of antecedent - consequent. More complex units such as the synusia and the associaton are not as appropriate to Principle A. Another principle, which we will designate Principle B, requires a more complex unit such as the homogeneous association and is an application of the principle of structure-function. Principle A tends to treat the whole as a simple collection of parts responding individually to their environment. Principle B, on the other hand, treats the whole as being composed of association parts functioning for the whole. Let us trace the effects of these two principles on ecological research.

Principle A

Principle A, which treats the individual as part, recognizes the existence of communities on the landscape. Gleason, as spokesman for the first principle, says:

> First, an association, or better one of those detached pieces of vegetation we may call a community, is a visible phenomenon. As such it has dimensions and area, and consequently boundary. While its area may be large, the community is nevertheless a very tangible thing, which may be mapped, surveyed, photographed and analyzed.[34]

According to this principle the community is not invested with processes of control over its composition and structure. Rather, the community is conceived to be the passive product of environment. In sup-

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34. H.A. Gleason, "The Individualistic Concept of the Plant Association," American Midland Naturalist, XXI (1939), 103.

port of this point Curtis[35] relies on Chamberlain, who has this to say:

> The natural flora may be regarded as the result of nature's experiments in crop raising through the thousands of years that have elapsed since the region became covered with vegetation. If we set aside the inherent nature of the several plants, the native vegetation may be regarded as the natural correlation of the combined agricultural influences of climate, soil, topography, drainage and underlying formations and their effect upon it. To determine the exact character of each of these agencies independently is a work of no little difficulty; and then to compare and combine their respective influences upon vegetation presents very great additional difficulties. But the experiments of nature furnish us in the native flora a practical correlation of them.[36]

Principle A has two further effects on the research which are of interest to us in exploring the role of principles in determining parts. In the first place it discriminates the individual organism and not the community as the respondent to the environment. Secondly, it renders it unnecessary to distinguish an individual and the species to which it belongs. Individuals are treated as being representative of species. Likewise, statements about species are considered to be sufficiently informative of the ecology of individuals. (The concept of ecotypic differentiation within a species brings the adequacy of this identification of individuals and species into question). We find Gleason arguing to the principle in species terms and, in Gleason's third point, we see the transition from species terms to individual terms without effect on the argument:

> The argument for the individualistic concept rests on a series of thesis each of which is so obvious, so well known, so universally understood and accepted by all ecologists, that none of them requires prolonged discussion.
>
> 1. Every species of plant has reproductive powers in excess of its need.
> 2. Every species of plant has some method of migration.

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35. J.T. Curtis, The Vegetation of Wisconsin: An Ordination of Plant Communities (Madison, Wis.: University of Wisconsin Press, 1939).

36. T.C. Chamberlain, "Native Vegetation of Eastern Wisconsin," Geology of Wisconsin, II (1877), cited by Curtis, p. 4.

3. The environment in any particular station is variable .... We at once arrive at the general theorem that each plant seizes and uses the particular time-period during which the environment is in a condition suitable to it.[37]

When we examine research conducted in terms of Principle A we find that communities are recognized and classified but that the recognition and classification is appropriately based on expediency. Since it is individual organisms and not communities that respond to environment communities are regarded simply as any area where a large number of species overlap to give the area a distinctive appearance.[38] As Gleason says, the community is merely "the visible expression, through the juxtaposition of individuals, of the same or different species."[39] Curtis, in his book The Vegetation of Wisconsin where he identifies thirty-four communities, agrees with this view of the community when he writes in the first chapter:

> Each of the component species has certain limits to the environmental variables within which it will thrive .... Those species which have similiar limits tend to grow together, but since the number of environmental factors which may influence the growth of plants is so very large, no two species have exactly the same limits. As a result, the communities which they form are not precise entities of fixed and unvarying composition, but rather are loose aggregations of species, whose make-up changes from place to place and from time to time in a more or less continuous fashion. The communities, therefore, and the entire vegetation which they compose, cannot be described in the exact language of physical science, but must be treated in a statistical manner as a continuous variable.

With this view of the community as a starting point Curtis goes on to point out the expedient nature of his final classification scheme:

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37. Gleason, "Individualistic Concept," pp. 93-97.

38. R.T. Patton, "The Factors Controlling the Distribution of Trees in Victoria," Royal Society of Victoria, Proceedings, XLII (1930), 154-210.

39. H.A. Gleason, "The Individualistic Concept of the Plant Association," Bulletin of the Torrey Botanical Club, LII (1926), 25.

40. Curtis, Vegetation of Wisconsin, p. 5.

> In view of the continuous nature of these interrelations, the delimitation of separate communities becomes a pragmatic matter, to be decided on convenience for the purpose at hand.[41]

and again:

> The terms, like the segments (communities-segments along a continuum) are purely arbitrary.[42]

We see that an investigator working in the problem area of classification and according to the dictates of Principle A is interested in communities; but his enquiry focuses on individuals. The required data are on the growth range of individual types on the landscape and on the spatial relations between individuals. This is clearly demonstrated by Curtis as he describes the techniques used by himself and other members of the Wisconsin school:

> In the quarter method ... the direction of the compass line is used as a bisect of the space around the point (reference point within the sample area) and this space is further divided by another imaginary line erected at right angles to the first, with the point as center. Within each of the quarters thus bisected, the closest tree to the point is chosen and its distance from the point determined .... All of the distances thus determined at all sampling points are summed and the total divided by four timesthe number of points used. The result equals the average distance between trees and is treated ... to obtain the average space occupied per tree. Species and basal areas are determined for each tree as before.[43]

In interpreting the data so collected, and while it is convenient for "practical purposes of study"[44] to classify communities, it is, according to Principle A more real to plot species distributions across their ranges of occurence. Thus, while his book is devoted to a classification of vegetation, Curtis gives a considerable number of pages to individual

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41. <u>Ibid</u>., p. 510.

42. <u>Ibid</u>.

43. <u>Ibid</u>., pp. 72-73

44. <u>Ibid</u>.

species plots. Of these he writes:

> Individual species when plotted against an ordinated gradient show Gaussian-type curves, with minima, optima and maxima. They indicate specific individuality in amplitude, range and position of the curves.[45]

Principle B

Turning to Principle B, which treats the association as part, we find that communities are recognized on the landscape. Clements, in one of his classic works written in terms of this principle, writes:

> The formation is the unit of vegetation. It is the climax community of a natural area in which the essential climatic relations are similar or identical . . . the formation is necessarily an organic entity, covering a definite area marked by a climatic climax. The climax formation is not an abstraction, bearing the same relation to its component associations that a genus does to a species. It is not a pigeon-hole in which are filed physiognomic associations gathered from all quarters of the earth.[46]

and again, he says the climax has a "visible unity."[47]

The early spokesmen for Principle B treat the association so seen as a real analogue of the organism of traditional biology. For example, Weaver and Clements use the term "social organism";[48] Tansley calls the community a "quasiorganism";[49] and Allee and others speak of the "supraorganism."[50] The community is further treated as a system composed of structures and functions operating in the interests of the community as a whole. Clements tells us that:

> The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity.

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45. Ibid., p. 481.

46. F.E. Clements, "Plant Succession: An Analysis of the Development of Vegetation," Carnegie Institute of Washington, Publication CXVII (1916), 126-27.

47. F.E. Clements, "Nature and Structure of the Climax," Journal of Ecology, XXIV (1936), 255. This quoted phrase indicates almost as well as we could ask the sense in which principles are "real" and yet are principles. That is, any factor identified by the principle would, in the case of scientific research, be "visible" or, if not visible in some literal sense, definable by "visible" parameters. So far it is real. It is also the case that other equally "visible" factors can be identified in other researches. In this sense, then, the identified factors are principles.

48. J.E. Weaver and F.E. Clements, Plant Ecology (2nd ed.; New York: McGraw-Hill, 1938), p. 207.

49. A.G. Tansley, "The Classicication of Vegetation and the Concept of Development," Journal of Ecology, VIII (1920), 123.

50. W.C. Allee, et.al., Principles of Animal Ecology (Philadelphia: W.B. Saunders and Co., 1949), p. 420.

> As an organism the formation arises grows, matures and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant.[51]

As is the case with structure-function principles in whatever discipline they are found or to whatever subject-matter they are applied, the entity in question is treated as being analyzable into parts. In the case of formations the part is the association. Clements writes:

> It (the formation) consists of associations covering a definite area marked by a climatic climax. It consists of associations, but these are actual parts of the area with distinct spatial relations.[52]

We see that parts as well as wholes are visible upon inspection. They may, in their turn, be treated as analogical wholes and thereby meet with one of the logical conditions of the structure-function principle; a condition pointed out by Schwab.[53] Following this condition Clements develops a terminology of parts composing the whole. These terms are the clan, the society, the consociation, the association and the formation.[54] We see Clements treating the association as analogical whole when he writes:

> The consociation is the unit of the association ... it (the consociation) is the most readily recognized of all communities .... The association thus becomes a group of two or more consociations.[55]

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51. F.E. Clements, Plant Succession and Indicators: A Definitive Edition of Plant Succession and Plant Indicators (New York: Wilson, 1928), p. 3.

52. Clements, Plant Succession, p. 127.

53. J.J. Schwab, Biology Teachers Handbook (New York: John Wiley and Sons, Inc., 1964), p. 188.

54. Clements, Plant Succession and Indicators, p. 140. Cf., cell type, tissue, organ system.

55. Ibid, p. 129.

According to the principle, formations are not merely collections of associations but, rather, are "organic entities."[56] In order to take account of this relationship between the whole and its parts the principle relies heavily on the concept of species dominance relations. Dominance, is defined by Clements as: " ... the ability of the characteristic life-form to produce a reaction sufficient to control the community for a period."[57] The method by which this control is brought about is various as we see in the following: "Dominance may mean the control of soil factors alone, primarily water content, of air factors, especially light, or of both water and light."[58] Thus, the unity and stability of the formation is, in large part, due to dominance. As Clements says, "The essential cause of stabilization (of the formation) is dominance."[59]

Following this line of thought, the associations are treated as being functionally related to one another through dominance. This is an interesting feature of Principle B since many authors criticize the use of dominant species in classification because of their wide geographic range and wide tolerances. Using the same fact Clements bases his classification on dominant species arguing that these create functional relations between associations. For example, we find Clements saying:

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56. _Ibid._, p. 3.

57. _Ibid._, p. 98.

58. _Ibid._

59. _Ibid._

> The association as here conceived bears the accepted relation to the formation. The term is restricted, however, to those climax communities which are associated regionally to constitute the formation. The associations agree with their formations in physiognomy and development, but differ in floristic and to a certain though unknown degree in habitat. Hence they are recognized chiefly by floristic differences. Associations are marked primarily by differences of species, less often by differences of genera. At the same time, their organic relation to each other in the climax unit or formation rests upon floristic identity to the extent of one or more dominants, as well as upon the fundamental development and the life forms. For example, the Bouteloua-peion contains two associations, the Bulbilis-Bouteloua-association, and the Hristida-Bouteloua-association. While the species of Bouteloua and Aristida are mostly in the two, one or more species of both genera are more or less common throughout.[60]

When we turn to research conducted in terms of Principle B we find that particular methods vary depending upon which level of part is under consideration. This is, of course, a commonplace in physiological researcn. Just as Harvey employs dissection techniques while modern "organelle" researchers employ the centrifuge -- both in response to structure-function terms -- so does the classifier vary his techniques depending on whether he is working with the formation or the society. Notwithstanding technical differences, the principle, at all levels of parts, demands that the researcher first circumscribe the part in question and then, by identifying dominant species, establish functional relations. As Weaver and Clements say:

> An airplane view of the continent of North America would reveal the fact that it is covered with three great types of vegetation, viz.; forest, scrub, and grassland. A closer scrutiny would reveal that these are themselves composed of strikingly different communities such as evergreen and deciduous forest which are found in climates equally different.[61]

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60. Clements, Plant Succession, p. 128.

61. Weaver and Clements, Plant Ecology, p. 478.

We see the method of circumscribing communities referred to as "primary survey"[62] by Tansley as he writes about the methods employed in his book The British Islands and Their Vegetation.[63] He has this to say:

> The method of primary survey on which the general classification of associations mainly rests, was to choose a stretch of country and then distinguish and map the communities that could be conveniently represented on the scale of one inch to one mile ... There is a good deal to be said for the constant direction of effort to the making of a good map, thought this is not, of course, to be regarded as the ultimate goal of any ecological work ... The making of a map focuses effort and compels the student to make up his mind about the status of the vegetation mapped ... It is certainly a sound principle that an extensive study or survey of a fairly large tract of land -- primary survey as it is called -- forms the best preliminary to intensive work. Such a survey gives a general knowledge of the types of vegetation and the conditions in which it occurs, and enables the student to choose areas or communities for more detailed study with skill and judgement.[64]

As the researcher begins to "choose areas or communities for more detailed study" new techniques are called for. For example, the quadrat is employed in order to identify the dominant species and, thereby, the functional relations contributing to the coherence of the community. We see the use of quadrats, and the species identified therein, illustrated in a report by Shantz:

> On the mesa the Andropogen scoparious consocies seems to be most primitive. In places not yet covered with vegetation, where the alluvium is nearest to what it seems to have been originally, this grass is most abundant and together with Eriocoma cuspidata is the first to disappear in passing from the exceedingly open association to the more stable or closed Bouteloua formation. Eriognum alatum, E. Jamesii, Tetraneuris glabriuscula, and Machaeranthera uchoracea are generally present; but since they extend into the true Bouteloua formation they are probably not as such a part of the primitive association as the plants mentioned above. The lem ridge vegetation is probably primitive as shown by the following quadrat:

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62. A.G. Tansley, Introduction to Plant Ecology (3d ed.; London: Allen and Unwin, 1954), p.80.

63. A.G. Tansley, The British Islands and Their Vegetation (Cambridge University Press, 1939).

64. Tansley, Plant Ecology, p. 88.

Lasquerella alpine 52	Orevcarya thysiflora 3
Gutiezzezia sarolthrae ... 5	Gaula coccinea 1
Lithospermum linearis 4	Machaeranthera cichoracea ... 1[65]

In contrast to the merely expedient classifications resulting from Principle A classifications resulting from Principle B are thought of as natural or real. Clements writes:

> In a natural i.e., a developmental system of classification it is clear that development must constitute the chief basis ... These climaxes of the existing flora are phylogenetically the descendents of a preceding flora ...[66]

and again:

> So, likewise, all the concepts of the formation and the methods of recognition so far employed are natural in so far as they use a natural process or response, and artificial in so far as they fail to correlate this with all the other equally natural and important processes. Taxonomic systems have become natural and hence fundamental in just the proportion that it has been possible to ground them upon development.[67]

To summarize, the use of Principle A in some papers and the use of Principle B in other papers for the problem of classification illustrates the roles of principles in providing terms for the conception of communities on the landscape; in establishing conditions to be fulfilled by parts in analysis, and thereby dictating the particular part employed; in establishing conditions of relationship between parts and between parts and the whole; in dictating the field techniques required in collecting classificatory data in the field; and in providing terms in which to conceive the classification achieved.

From the above examples we see that different principles give rise to different bodies of knowledge. As is the case for different problems it becomes extremely difficult to join such bodies of knowledge in one coherent whole. We later show how problems and principles together determine significantly different patterns of enquiry and we show how these patterns

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65. I.H. Shantz, "A Study of the Vegetation of the Mesa Region East of Pikes Peak: The Bouteloua Formation," Botanical Gazette, XLII (1906), 189.

66. Clements, "Plant Succession," p. 177.

67. Ibid. p. 124.

may be used to articulate the diversity of knowledge forms in ecology.

The Creation of Parts in Terms of a Principle

In addition to the role of principles in selecting among recognized community parts they may also require new parts. The minimally complex unit, "synusia," is a case in point. (Synusiae are layers or strata or vegetation as, for example, the herbaceous layer is a forest). The term "synusia" was created in response to certain problems in classification. Let us see how this came about.

In the problem area of classification and taxonomy the structure-function principle dictates that the appropriate part shall be the homogeneous association. We have already shown this to be the case in our discussion of Principle B. There are certain difficulties in working with this unit however. The condition of homogeneity is necessary and as Nordhagen says:

> It can readily be maintained that phytosociology would be impossible without the existence in nature of homogeneous, or relatively homogeneous overgrown areas.[68]

Nevertheless, since the association embodies the total vegetation in an area, the condition of homogeneity is never met, provided the researcher looks closely enough. The fact of local heterogeneity is well documented, especially by research in the problem area of distribution. Much of the research conducted in terms of Principle A also demonstrates the fact.

Two cases will illustrate our point. The first emphasizes spatial variation in the habitat while the second emphasizes spatial variation in

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68. R. Nordhagen, "Die Vegetation und Flora des Sylenegebietes: I. Die Vegetation; Skrift Norske Videnskaps-Akad. Oslo, 1927," Mat. Naturvid. KL., I (1928) cited by T. Lipmaa, "The Unistratal Concept of Plant Communities," American Midland Naturalist, XXI (1939), 113.

the organisms themselves. In the introduction to the first study the authors emphasize the apparent homogeneity of the area studied:

> In each woodland, areas were chosen which appeared relatively homogeneous and yet were large enough to be representative of a forest type. The selected woodland sites were, as regards topography and vegetation, probably the most uniform to be found in the Lake District and consisted of two stands of fairly mature oak ...[69]

In this research samples are laid out on a subplot within plot within block basis; the sizes being 25 cm.^{2}, 1 m.^{2} and 10 m.^{2} respectively. Cores of litter, vegetation and soil are taken. The researchers find very high coefficients of variability for soil factors. For example, the variation of pH is greater between subplots than between blocks and obscures monthly variation in pH. Side-by-side subplots commonly differ in pH from one another by as much as one pH unit.

The second study is in the tradition of Principle B in that vegetation types, defined according to the homogeneity of species composition, are treated. As the authors say in their introduction:

> Emphasis has also been placed upon the homogeneity of the vegetation type, by which is meant a more or less uniform probability of encountering a given assemblage of species in any sample taken from the type.[70]

and again:

> After considerable preliminary study, a number of types of vegetation were recognized on the basis of physiognomic differences.[71]

In this research the survey area is an old field approximately 330 m. by 200 m. in size. Within this area, and in accordance with the preliminary survey, 65 plots ranging in size from 4 m.^{2} to 15 m.^{2} are set

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69. J.C. Frankland, J.D. Ovington, and C.C. McCrae, "Spatial and Seasonal Variations in Soil, Litter and Ground Vegetation in Some Lake District Woodlands," Journal of Ecology, LI (1963), 97.

70. F.C. Evans and E. Dahl, "The Vegetational Structure of an Abandoned Field in Southeastern Michigan and Its Relation to Environmental Factors," Ecology, XXXVI (1955), 685.

71. Ibid, p. 689.

out. A complete list of species for each plot is recorded. Following this procedure eleven, homogeneous, vegetation types in approximately fifteen acres are identified. In the face of evidence such as this Dahl and Hadac conclude that:

> In nature plant communities are never fully homogeneous i.e., the density of the species of importance by the characterization of the community, especially the dominant species, have not exactly the same density in all parts of the area. We may thus talk of more or less homogenous plant conditions.[72]

Workers in the area of classification and taxonomy have not, however, been satisfied with "more or less homogeneous plant communities." The adequacy of Principle B is challenged when faced with the fact of heterogeneity. There have been three responses to this challenge to Principle B, of which the third is of most interest to us now: (1) rejection of Principle B in favor of another, (2) addition of ad hoc terms and conditions to Principle B, (3) systematic reconstruction of Principle B.

The first of these reactions is seen in our discussion of Principle A. Prior to his explication of Principle A, Gleason had demonstrated local variability in vegetation[73] and in Curtis' classification of the vegetation of Wisconsin the fact of heterogeneity plays an important role.[74] It is this fact that leads Curtis to treat vegetation as continuous, and to treat the ultimate classification achieved as arbitrary.

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72. Dahl and E. Hadac, "Homogeneity of Plant Communities," Studia bot. Cechosl., X (1949), cited by K. Kershaw, Quantitative and Dynamic Ecology (New York: American Elsevier Publishing Company, 1964), p. 134.

73. H.A. Gleason, "Some Applications of the Quadrat Method," Bulletin of the Torrey Botanical Club, LIII (1920), 7-26.

74. Curtis, Vegetation of Wisconsin.

The first reaction to heterogeneity is also illustrated by a number of writers who use a rational principle and who distinguish between "abstract" and "concrete" communities. Schwab has this to say about the rational argument:

> Principles of this kind require that the subject of interest must be seen as given its character by its place in some larger determinative whole or by some ratio imposed from without.[75]

Rowe, for example, thinks of the ecosystem as one of a series of continuous inclusions i.e., ecosystem within ecosystem within ecosystem ranging from the cell to the ecosphere.[76] A rational principle is insisted upon throughout since even the minimal element is a system and is not reducible to merely logistic terms. Somewhat similarly, Nichols thinks of the classificatory categories, e.g., formation, as abstractions rather than as concrete entities.[77]

The second reaction to heterogeneity, the use of ad hoc terms and conditions, is illustrated by Clements. He appends such terms as "pre-climax" and "post-climax" to communities which do not fit the basic set of climax community classes.[78]

The systematic reconstruction of principles, is illustrated by the creation and use of the concept of synusia.
We find Cain, a spokesman for the synusial approach, recognizing the problem posed by heterogeneity in the following:

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75. Schwab, "What do Scientists do?" p. 8.

76. J.S. Rowe, "The Level of Integration Concept and Ecology," Ecology, XLII (1961), 420-27.

77. Curtis, Vegetation of Wisconsin.

78. Clements, "Nature and Structure," pp. 267-29.

... the present treatment of associations results in communities of extremely great differences in complexity being placed on an equal basis as associations ... Furthermore, a many-layered phytocoenose will show considerable variation as to its floristic assemblage ...[79]

Lipmaa, who uses the terms "one layered community" or "union" rather than synusia, argues for the synusia approach on the grounds of its homogeneity. He writes:

The simplicity of unions regarding layering is emphasized here since they are always based on the dominance of a single or two related life forms.[80]

Thus, according to the proponents of synusiae, while it is difficult, "if not impossible"[81] to classify associations as a whole it is possible to achieve a meaningful, in fact natural,[82] classification based on the synusial units. Cain and Penfound argue for focusing enquiry on synusiae in the following:

It is obvious from previous work that the best method of studying a phytocoenosis is to study the synusiae separately and, on the basis of this knowledge, to synthesize a picture of the association.[83]

Based on this new unit several variant reconstructions of our original Principle B are effected. For Lipmaa synusiae are largely autonomous parts within the association.[84] As such he rejects the original

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79. S.A. Cain, "Synusiae as a Basis in Plant Sociological Field Work," American Midland Naturalist, XVII (1936), 668.

80. T. Lipmaa, "The Unistratal Concept of Plant Communities," American Midland Naturalist, XXI (1939), 119.

81. T. Lipmaa, "Une Analysis des Forets de l'Ile Estonienne d Abruka (Abro) sur la Basedes Associations," Acts Inst. et Horti Bot. Univ. Tartuensis, III (1935), cited by Cain, "Synusiae as a Basis," p. 665.

82. Cain, "Synusiae as a Basis," p. 666.

83. S.A. Cain and W.T. Penfound, "Aceretum rubri: The Red Maple Swamp Forest of Central Long Island," American Midland Naturalist, XIX (1938), 391.

84. Lipmaa, "Une Analysis des Forets," p. 146, cited by Cain, "Synusiae as a Basis," p. 665.

association and offers a classification of the synusiae themselves. Cain is concerned about vertical interactions between the synusiae.[85] He tends to side with Lipmaa on the question of autonomy, but, nevertheless, maintains a focus on the association. By and large, for Cain, associations are collections of synusiae. Daubenmire, on the other hand, treats the association as a set of interacting parts, the synusiae, and maintains the focus of Principle B on the association as a whole.[86] He writes:

> The association is considered the basic unit of vegetation classification. It embraces all unions that are superimposed on the same area, and each distinctive combination is ordinarily considered a separate association. Such an aggregation of union constitutes a phytocoenose.[87]

Daubenmire's choice of the word "aggregation" is unfortunate since this implies a concept of the association as being a mere collection of synusiae; a concept he does not employ. For Daubenmire synusiae are only "partially independent."[88]

In each of these three reconstructions of principle, and regardless of the interesting differences among them, we see a common logical condition. The common condition is the principled requirement for a homogeneous association unit upon which to found classification. The concept of synusia was created to meet the demand of this requirement as a consequence of the fact of heterogeneity.

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85. S.A. Cain, "Studies on Virgin Hardwood Forest: II. A Comparison of Quadrat Sizes in a Quantitive Phytosociological Study of Nash's Woods, Posey County, Indiana," American Midland Naturalist, XV (1934), 529-66.

86. R. Daubenmire, "Forest Vegetation of Northern Idaho and Adjacent Washington and Its Bearing on Concepts of Vegetation Classification," Ecological Monographs, XXII (1952), 301-30.

87. Ibid., p. 302.

88. Ibid., p. 302.