DOCUMENT RESUME

ED 040 078 SE 008 791

AUTHOR	Connelly, F. Michael
TITLE	Patterns of Enquiry in Ecology: 2: Principles and Patterns of Ecological Enquiry.
INSTITUTION	Chicago Univ., Ill.
PUB DATE	14 May 70
NOTE	45p.
EDRS PRICE	EDRS Price MF-$0.25 HC-$2.35
DESCRIPTORS	*Biology, *Ecology, *Logic, *Scientific Methodology, *Scientific Research

ABSTRACT

This is the second paper in a two-part series describing the patterns of inquiry used in ecology. Three classes of research parts are identified from the literature: individual organisms or species, pairs of organisms or species, and groups of organisms or species. Research emphasizing these parts rather than the community as a whole is analyzed in terms of the principles of biological inquiry discussed in the first paper. A second section of the paper shows how accounts of the community as a whole can be built from the results of research on parts, and discusses different conceptions of the relationship between parts and whole. The third section analyzes research beginning with an emphasis on the whole. A summary of the patterns of inquiry found in ecology relates the four principles of inquiry to the five problem areas defined in the first paper, giving eighteen different patterns of inquiry. (EB)

May 14/70

Patterns of Enquiry in Ecology: II. Principles and Patterns of Ecological Enquiry

F. Michael Connelly

This is the second paper in a two part series describing the patterns of enquiry used in ecology. Part I described the principles of biological enquiry generally and the problem areas of ecological enquiry.[1] Both problems and principles were shown to give rise to certain characteristic patterns of ecological enquiry. In part II we describe and summarize the principles and patterns of ecological enquiry.

PRINCIPLES OF ECOLOGY

This section is divided into three sub-parts. In the first sub-section we set out three classes of research parts found in the literature --individual organisms or species, pairs of organisms or species and groups of organisms or species. The papers examined in the first sub-section are ones in which the overwhelming emphasis of the research is on the part and not on the community. The research on each of these parts proceeds in different ways according to one or another modification of the principles of biology. Most papers treat this research as being preliminary to more adequate accounts of communities. Accordingly, in the second sub-section we show how the results of studies conducted in terms of the three classes of parts are

1. F. Michael Connelly "Patterns of Enquiry in Ecology: I Principles of Biological Enquiry and Problems of Ecological Enquiry."

used to give accounts of the community as a whole. Our third sub-section describes the various conceptions used by ecologists in research beginning with communities as a whole.

Research with an Emphasis on the Part

The Individual Organism

Research on the individual has a special place in the literature of ecology. The difference between approaches to the individual and all other approaches described herein is reflected in the distinction between "autecology" and "synecology." In one approach to the individual, environmental factors are identified and correlated with the requirements or distribution of a species. Illustrative titles are, "Some Observations on the Relation Between the Hydrogen-Ion Concentration of the Soil and Plant Distribution,"[2] and "Physical Site Factors Influencing Annual Production of True Mountain Mahogany, Cerocarpus montanus."[3] Typically the researcher describes the observed relationship in terms of the dependence of the organism on the environmental factor. As such this research treats its material in terms of antecedent and consequent.

A second conception which focuses on the individual treats the organism in terms of multiple relations with environment. This is seen in Billings'

---

2. H. E. G. Emmett and E. Ashby, "Some Observations on the Relation Between the Hydrogen-Ion Concentration of the Soil and Plant Distribution," Annals of Botany, XLVIII (1934), 869-76.

3. D. E. Medin, "Physiological Site Factors Influencing Annual Production of True Mahogany, Cerocarpus montanus," Ecology, XLI (1960), 454-69.

conception of a "holocoenotic principle" in which he diagrams an individual organism in the center of a surrounding environment made up of biotic and -biotic elements.[4] This conception leads to the study of ecological life histories for which three approaches are found in the literature. In one of these approaches the research proceeds by identifying the variety of environmental conditions prerequisite to an aspect of the life cycle. For example, in a study of tiger beetle reproduction Shelford finds that:

> . . . for the egg-laying to take place the surrounding temperature and light must both be suitable, the soil must be moist, probably also warm, and must satisfy the ovipositor tests with respect to several factors . . . The success of reproduction depends, then, upon the qualitative and quantitative completeness of the complex of conditions.[5]

This research uses an antecedent consequent principle in which a single consequent has a complex of antecedents.

Another approach to the study of life histories correlates changes in organism behavior with changes in environment over a suitable period of time. For example, in a study of alpine sorrell Mooney and Billings find that as the days become shorter the decrease in day length causes a dormant bud to be formed.[6] Again, this is a study in antecedents and consequents but now with respect to events and changes in factors.

Still another approach to the study of life histories identifies the repertory of functional morphological adaptations available to an organism

---

4. Billings, "Environmental Complex."

5. Victor E. Shelford, "Physiological Animal Geography," Journal of Morphology, XXII (1911), 598.

6. H. A. Mooney and W. D. Billings, "Comparative Physiological Ecology of Arctic and Alpine Populations of Oxyria dignya," Ecological Monographs, XXXI (1961), 1-29.

when the organism is confronted with a variable environment. Functional adaption is illustrated by the gnatcatcher study earlier described.[7] Morphological adaptation is illustrated in a review paper by Thorsen who shows that many species of marine snails can produce two kinds of eggs, small ones with little yolk which produce pelagic larvae, and large yolk-rich eggs which produce young snails, skipping the larval stage. The percentage of eggs producing pelagic larvae decreases from warm to cold environments. Artic populations produce only yolk-rich eggs. Thorsen is also treating functional adaptation as is seen in his emphasis on the production of young snails which skip the larval stage.[8] To the extent that Thorsen emphasizes a fixed environmental continuum his approach is in terms of antecedents and consequents. However, his description of the consequent in terms of functional and morphological adaptive possibilities indicates a concern for regulation.

Aside from the research on life histories few papers are found in the literature which focus directly on the multiple relations of an organism with its environment. As Dice remarks:

> Far too little is yet known about the relations between organisms and their environment to enable one to predict how any individual is going to react to any particular combination of physical factors.[9]

A third approach to the ecological treatment of individuals focuses on a factor controlled by a cycle of events. The cycle has two main parts, the

---

7. Connelly, "Patterns: I", pp. 23-24.

8. G. Thorsen, "Reproductive and Larval Ecology of Marine Bottom Invertebrates," Biological Review, XXV (1950), 1-45.

9. Dice, Naturual Communities, p. 102.

organism and its immediate environment. The controlled factor may enter and leave the cycle at various places. The cycle is made up of a series of storage points which also serve as translocation points. Thus, nitrogen is stored in leaves and is transferred from here to soil arthropods at the time of leaf fall. Research proceeds by identifying the relevant input, translocation and output points for the factor being cycled. Research may terminate at this point or it may proceed to quantitatively describe the rate of translocation from point to point. Illustrative titles are, "Nutrient Cycles Under Moist Tropical Forest"[10] and, "Nitrogen Requirements and the Biological Cycling of Nitrogen in Douglas-Fir Stands in Relationship to the Effects of Nitrogen Fertilization."[11] This is a study of homeostasis in which the factor held relatively constant is the amount of the element available for reutilization by the plant and the mechanism is the cycle and its biological controls.

Pairs of Organisms

The emphasis on pairs of organisms may or may not be done with reference to the environment. The simplest approach to species pairs establishes the coassociation between two or more species by presence and absence or, perhaps, abundance data. The species are compared according to their tolerances for one or another environmental factor. The coassociation is accounted for in

---

10. P.H. Nye, "Nutrient Cycles Under Moist Tropical Forest," Plant and Soil, (1961), 333-46.

11. P.E. Heilman and S.P. Gessel, "Nitrogen Requirements and the Biological Cycling of Nitrogen in Douglas-Fir Stands in Relationship to The Effects of Nitrogen Fertilization," Plant and Soil, XVIII (1963), 386-402.

terms of overlapping tolerances. Curtis, for example, sets out transects along an environmental continuum, e.g. low to high soil moisture levels, and plots overlapping bell shaped distribution curves for various species.[12] As such, this is a study in antecedents and consequents where a single antecedent gives rise to more than one consequent.

A second approach to species pairs focuses on the interactions between them. Here, pairs of species may be thought of as containing the interactions that may be missing from the study of a single species. Berkholder lists nine such interactions according to classes of outcomes for the species, namely, positive, negative or neutral.[13] Odum reduces these six types and names each with such terms as competition, predation and symbiosis.[14] The mechanisms of interaction are of two types, direct and indirect (through modification of the mutual environment). In one approach to the study of these interactions the research establishes one or more experimental situations by varying a set of environmental factors. The two species are introduced to the system and the relative proportions of each are plotted over time. Park's research on competition between species of flour beetles illustrates this approach. Park does not examine the various and perhaps different uses of the environment by the species but, rather:

> He (the reader) may ... view interspecies competition merely as those new events that emerge when the two species populations coassociate.[15]

---

12. Curtis, Vegetation of Wisconsin.

13. Paul R. Berkholder, "Cooperation and Conflict Among Primitive Organisms," American Scientist, XL (1952), 601-30.

14. Eugene P. Odum, Fundamental of Ecology (2d. ed.; Philadelphia: W.B. Saunders and Co., 1959), p. 225.

15. Thomas Park, "Experimental Studies of Interspecies Competition: II. Temperature, Humidity and Competition in Two Species of Tribolium," Physiological Zoology, XXVII (1954), p. 178.

As such this conception is Schwab's "black box" study of homeostasis.[16]

Other studies of species interaction focus on the mechanism of the interaction. Such studies may manipulate and measure one or more environmental factors in common or they may compare the life histories of the interacting species. As an example of the former procedure Blackman and Tempelman vary the relative densities of cereal and weeds as well as the level of soil nutrients. They then determine the comparative growth and mineral contents of the cereals.[17] The latter procedure is seen in Butler's account of cycles of fur bearing animals in Canada. These species interact in predator-prey coactions, and Butler is able to show that over a period of years the population cycles are similar but slightly out of phase. Thus, the lynx cycle follows the hare cycle.[18] In each of these procedures the homeostatic mechanism is studied. The procedure differs here in that the second requires a constancy of relationship between the species and, over time, a constancy for each species. The first procedure has no such requirement.

In general, experimental and field studies of species interactions differ in focus. The field study characteristically focuses on the fact of population control, while the experimental study attempts to generate control situations. The conditions of any such situation amount to the mechanism of control.

---

16. Joseph J. Schwab, personal communication, 1968.

17. M.E. Blackman and W.G. Tempelman, "The Nature of Competition Between Cereal Crops and Annual Weeds," Journal of Agricultural Research XXVIII (1938), 247-71.

18. L. Butler, "The Nature of Cycles in Populations of Canadian Mammals," Canadian Journal of Zoology, XXXI (1953), 242-62.

Groups of Organisms

One approach to groups of organisms identifies the ecotype or groups of ecotypes as the appropriate part. (An ecotype is a genetically distinct species variant adapted to a local habitat.) Research proceeds by identifying different behavioral, physiologic or other phenotypic forms of a species under different natural conditions. The variants may, in extreme cases such as those in Cyclops as reviewed by Yeatman, be different enough to be given different species classifications.[19]

In these cases the evidence is lacking as to whether the differences are due to different genotypes or to different items in a morphological repertory. Accordingly, transplant experiments are required to make this separation. In some studies the research looks for 'ecoclines" (genetic gradients along an environmental continuum). This is seen in Böcher's "Racial Divergencies in Prunella vulgaris in Relation to Habitat and Climate," a study of race in relation to habitat and climate.[20] In other studies, research emphasizes the "ecotype" as opposed to the "ecocline." Clausen and Hiesey, for example, identify four subspecies for Potentilla glandulosa, each with several ecotypes. Each subspecies is characterized by its distribution, habitat, internal variation and self-compatibility.[21] Such studies are structural in focus although the results may be given

---

19. Harry C. Yeatman, "American Cyclopoid Copepods of the Veridis-Vernalis Group (including a Description of Cyclops Carolinianus n. sp.)," American Midland Naturalist, XXXII (1944), p. 31.

20. T.W. Böcher, "Racial Divergencies in Prunella vulgaris, in Relation to Habitat and Climate." New Phytologist, XLVIII (1949), 285-324.

21. J. Clausen and W.M. Hiesey, "Experimental Studies on the Nature of Species: IV. Genetic Structure of Ecological Races," Carnegie Institute of Washington, Publication DCXV (1958), p. 6.

a functional interpretation. Turesson, for example, remarks that:

> . . . the differentiation of the plant species into the different hereditary habitat types (ecotypes) . . . cannot be adequately accounted for by recourse to such sporadic variability preserved by chance isolation. On the contrary . . . these habitat types in all probability represent definite genotypical responses of the plant species to definite habitat factors.[22]

Böcher's research is a study on antecedents and consequents where the environmental gradient plays the role of antecedent and the "ecocline" plays the role of consequent. Clausen and Hiesey's research is a study on species regulation in which the environment is treated as a given and controller.

Another group treated in ecological enquiry is the synusia. We earlier showed how the synusia is used in ecological enquiry.[23] Suffice it to say that the species making up any synusia are assumed to have similar physiological requirements. As such this group is accounted for in terms similar to those seen in our first approach to the coassociation of species pairs. However, the synusia is a unit of classification and is not studied by the antecedent-consequent methods used on the species pairs. Rather, research proceeds by dividing communities into vertical layers, the synusia, and then characterizing and classifying the synusia according to their species composition. As such this is a structure-function approach using a structural focus.

---

22. G. Turesson, "The Genotypical Response of the Plant Species to the Habitat," Hereditas, III (1922), p. 344.

23. Connelly, "Patterns: I", pp. 35-40.

Accounts of Communities as a Whole Using The Results of Research on Parts

The papers of the first sub-section are primarily concerned to give an account of one or another of the three kinds of community parts - individual organism, pairs of organisms and groups of organisms. A review of the literature shows that the knowledge so gained is used in diverse ways in other writings to give accounts of communities as a whole. This use depends, of course, on the writer's conception of the relations among parts and between these and the whole. The possible relations are described by Schwab in his triple distinction between reduction, regulation and a view intermediate to these two.[24]

According to Schwab the reduction view treats an organization as if its properties arise from the properties of its individual parts as seen in the examination of these parts in isolation from one another. The middle view also takes the position that the constituent parts make important contributions to the organization of the whole and, therefore, that the parts be studied in their own right. The position further holds, however, that the parts must also be examined in interaction with one another. Behind this position is either of two alternative notions. First, the view may be taken that although the parts are the only resource for organization, there are many properties of parts which are latent when the parts are in isolation. The second view holds that the properties come into existence as a consequence of interactive relations and not merely as latent properties of

---

24. Joseph J. Schwab, personal communication, 1968.

the relata. To a certain extent this last distinction is of no use to us since both positions dictate the same investigation, namely a study of the parts in relation to one another. Finally, in regulation the parts are treated as if the properties they have in isolation are subject to considerable alternation by the act of being be-neighbored. In this view a study of th. ;a-ts in isolation is relatively unimportant and a study of the whole, whether by one to one interactions or in more complex arrays, becomes the primary concern.

Reductive view of the relationship of part and whole

In some cases the community is virtually dispensed with. Thus, Clarke conceives of communities as being "due to mere coincidence of range . . . and not to any community structure.[25] We earlier saw a similar conception where Lipmaa treats communities in terms of a summation of their component synusia.[26] These are reductive cases where the collective knowledge of the parts in isolation amounts to an adequate knowledge of the community.

Another reductive use of research on parts is to treat the part as a model of the community. Three such approaches are seen in the literature. One approach which elevates the reductive unit to an analogue of the community. is found in the "systems" literature on computer simulation. Holling, for example, says that predation "reflects all the properties of a larger system."[27]

---

25. E. J. Clarke, "Studies in the Ecology of British Grasshoppers," Transactions of the Royal Entomological Society of London, XCIX (1946), 173-222.

26. Connelly, "Patterns: I", p. 39.

27. Crawford S. Holling, "The Strategy of Building Models of Complex Ecological Systems," in Systems Analysis in Ecology, ed. by Kenneth E. F. Watt (New York: Academic Press, Inc., 1966), p. 201.

Holling uses Millsian techniques in a variety of predator-prey interactions and constructs a generalized model of predation. The model is used in two ways. First, since the model contains the properties of communities as a whole, manipulation of the variables in the model tells us how communities react to comparable natural variations. Second, the model is used for specific predator-prey systems by deleting the inappropriate interactions in the generalized model. This approach represents Schwab's "molecular reduction."[28] Closely related to this form of molecular reduction is one in which mathematical models are fitted to the laboratory determined experimental results. This approach is common in demographic studies and in studies on species pairs. Gause, for example, derives competition equations for two species of yeast on an unreplenished medium. He then modifies the equations by assuming that the organisms of both populations are being removed at a given rate.[29] Slobodkin illustrates the sense in which these equations and their modification are used as community models when he writes that:

> This factor (the rate of removal) can be thought of either as a non-specific predator or as a washing away or replacement of a constant fraction of the experimental volume . . . for example, the overflow of a small pool in a stream.[30]

Others, such as Park in his paper "The Laboratory Population as a Test of a Comprehensive Ecological System," think of the mathematical expressions as models of entire ecosystems, albeit highly simplified systems.[31]

---

28. Schwab, "What Do Scientists Do?" p. 4.

29. G. F. Gause, La Theorie Mathematique de la Lutte Pour la Vie (Paris: Hermann et Cie, 1935), cited by Lawrence B. Slobodkin, Growth and Regulation of Animal Populations (Chicago: Holt, Rinehart and Winston, 1961), pp.71-81.

30. Solbodkin, Growth and Regulation, p. 75.

31. T. Park, "The Laboratory Population as a Test of a Comprehensive Ecological System," Quarterly Review of Biology, XVI (1941), 440-61.

Still another reductive approach through models is seen in the individually based studies on nutrient cycling. Here, the elements and quantitative relations of the cycle are expressed on a per unit of area basis. In effect, the expression of results in these terms amounts to treating the cycle as a sample of the community as a whole. Results for the sample are merely multiplied by the appropriate factor for any community. The action of the cycle in this approach is attributed to generalized processes and not to the parts per se. Thus, in his paper, "Plant Nutrients in Hard Beach: III. The Cycle of Nutrients," Miller expresses his results on a "pounds per acre per month basis" and uses such terms as "leaf fall" and "recreation" as functional components in the cycle.[32]

Intermediate views of the relation of part and whole

In other cases the part becomes an antecedent or consequent element. Here, the community is conceived as a network of chains of antecedent-consequent events in which the part is treated as both acting and reacting. Pimental speaks for this view when he says:

> We know that each plant and animal species form a cog in the total machinery of the community system. Each acts with and reacts to other members within the vast interlocking network of the total.[33]

---

32. R. B. Miller, "Plant Nutrients in Hard Beech" III. The Cycle of Nutrients," New Zealand Journal of Science, VI (1963), 388-413.

33. David Pimental, "Complexity of Ecological Systems," in Systems Analysis in Ecology, ed. by Kenneth E. F. Watt (New York: Academic Press, Inc., 1966), p. 16.

The construction of food webs is characteristic of this approach and may be seen in almost any textbook.

The part becomes a functional element in other papers. This occurs in two ways. First, the part is used in a structure-function conception of the community. Thus, Clements sees pairs of species as forming a functional unit. On the subject of competition he says that "it is the controlling function in successional development."[34]

A second way of treating the part as a functional unit is seen in homeostatic conceptions of the community where the homeostatic mechanism is the unit. This approach is typically seen in the treatment of interacting species where the interaction is seen as a mechanism of numbers control in the "balance of nature." For example, in a section on "the balance of nature" in his book Dice writes:

> The most effective regulatory mechanisms in a community are those density-dependent mortality producing agencies that reduce the numbers of a given species when it is too abundant and that lesson the mortality pressure against the species when the numbers are low, thus allowing it to survive. Predation, parasitism, disease, competition, and simillar mechanisms are usually density-dependent. . . . By their damping effect on the swings of population abundance these density-dependent regulatory mechanisms tend to maintain community stability.[35]

In each of the three treated views of the relationship of part and whole--the part as an antecedent-consequent element, the part as a structure-function unit and the part as a homeostatic unit--the parts are seen in relation to one another.

---

34. Clements, Plant Succession and Indicators, p. 3.

35. Dice, Natural Communities, p. 345.

Terms and lines of research in accounting for part and whole

Our treatment illustrates still another aspect of the way in which the results of research on parts is used, namely that research conducted in one set of terms may be used to account for communities in the same or different terms. Furthermore, several lines of research may be used by a conception of the community. Let us illustrate these various uses.

Curtis' conception of communities as being collections of species and his resulting "arbitrary" classification of Wisconsin forest communities illustrates the use of the same terms-antecedent and consequent-to account for both the part and the community.[36] Dice's treatment of species pairs as community homeostatic mechanisms illustrates the same point for homeostasis.[37] Clements, on the other hand, treats the interaction between species pairs as being community functions.[38] Thus, homeostasis studies of parts are used to account for communities as a whole, namely in homeostatic terms and in structure-function terms. The same thing is seen for the synusia where, as was earlier seen, Daubenmire uses the synusia as a functional unit and Lipmaa uses the synusia as a part in a collection.[39]

Ovington's review paper, "Quantitative Ecology and the Woodland Ecosystem Concept," illustrates the use of several research approaches to parts in treating communities in terms of a single principle.[40] The paper,

---

36. Curtis, Vegetation of Wisconsin.

37. Dice, Natural Communities.

38. Clements, Plant Succession and Indicators.

39. Connelly, "Patterns: I", pp. 39-40

40. J.D. Ovington, "Quantitative Ecology and the Woodland Ecosystem Concept," Advances in Ecological Research, I (1962), 103-92.

furthermore, illustrates Schwab's "fluid enquiry" in that Ovington advances a conception of the ecosystem in terms of which he reviews the research literature.[41]

In Ovington's case the principle is a modification of regulation. For Ovington, ecosystems are open systems with interflows of matter and energy between systems. Matter is accumulated, transformed and translocated in ecosystems. Ecosystems have two parts, the biotic component and the "microenvironment," the whole of which is related to the "macroenvironment." Ecosystems are internally variable in space--ecosystems form "continua" on the landscape--and in time--"there may be no long-term balance of the nutrient capital." Ecosystem boundaries are vague and the kind of thing that can play the role of whole may be "an ecological unit of any rank." Ovington agrees with Rowe that we can "think of a hierarchy of increasingly cumulative ecosystems.[42] Not all of these aspects are made use of by Ovington in his review. In fact when he treats the various lines of research--organic-matter, energy, water, minerals--he does so in separate sections of the paper even though his intention is to stress the "fundamental unity" of the processes associated with nutrition and metabolism and energetics. Ovington's account is given in terms of the productivity of the system as a whole as well as its various strata and not in terms of the parts on which the research is based.

Ovington's regulatory stress on internal variability in time and space illustrates the third conception of the relations between part and whole. Here, knowledge of the parts is insufficient since the parts vary at other times and at other places.

---

41. Schwab, "What do Scientists Do?" pp. 21-22.

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

Research Beginning with an Emphasis on the Whole

With the exception of genecology the problem areas are well represented by papers concerned with communities. The exception of genecology may, in part, be due to the time required to conduct an adequate experiment. In the short run, organisms must be transplanted and allowed to develop, usually for several generations. In the long run, depending on the life cycle of the species composing the community in question, a prohibitive amount of time may be required to study the conditions and mechanisms by which various ecotypic organizations are developed. However, genecological problems could be studied more frequently and with a wider variety of principles than is now the case. In this respect it is significant that McMillan was awarded the 1960 George Mercer Award of the Ecological Society of America for his paper "The Role of Ecotypic Variation in the Distribution of the Central Grassland of North America."[43] The following illustrates some of the kinds of genecological problems that might be studied. To determine:

. . . the mosaic of competitive intensities between the ecotypes of two species and how these modify dominance and other interdependent relations.

. . . the community size and habitat diversity necessary to bring about various levels and groupings of ecotypic differentiation.

. . . the changing ecotypic structure in communities undergoing succession or when confronted with changing environments.

. . . the extent to which known functional repertories, e.g., acting in different energetic capacities, may be accounted for in terms of ecotypic adaptation.

. . . (following the last problem) the possibility and extent of different functional community organizations with similar species composition.

---

43. Calvin McMillan, "The Role of Ecotypic Variation in the Distribution of the Central Grassland of North American," Ecological Monographs, XXXIX (1959), 285-309.

The literature is not, of course, without writings which point to a theoretical basis for questions related to the maintenance, succession and evolution of communities in genecological terms. Darlington's book, The Evolution of Genetic Systems is frequently referred to in this respect.[44] An example of this is seen in Heslop-Harrison who discusses the migration of forest communities northward after the last ice-age. For instance, he writes:

> Moreover, the "optimum" phenotype of the open marginal community may not be that of the main closed community, so the phenotypic distribution of the colonists may not only reveal a higher variance but a different mean. The exact implications of this situation have not hither-to been worked out, although it may be supposed that the effect will be transient since the progressive closing of the community may be expected to restore the original balance of selective forces.[45]

Characteristics of communities as a whole

According to Schwab the attempt to identify characteristics of the subject-matter as a whole is the first step in any discipline whose subject-matter is concerned with a process which has a beginning, middle and end. Various measures are used to indicate the degree of maturity or stability of the subject-matter. Thus, there are measures of emotional maturity, physiological maturity and growth maturity.[46] Communities fit the criterion of a subject-matter concerned with a process in their succession to maturity. Margalef states the case in ecology when he says:

> For a quantitative measure of structure it is convenient to select a measure that suggests this historical character, for instance, maturity. In general, we may speak of a more complex system as a

---

44. C. D. Darlington, The Evolution of Genetic Systems (2d. ed., rev.; New York: Basic Books Inc., 1958).

45. J. Heslop-Harrison, "Forty Years of Genecology," Advances in Ecological Research, I (1962), p. 201.

46. Joseph J. Schwab, personal communication, 1968.

> more mature ecosystem. . . . The term maturity suggests a trend . . . maturity, then, is a quality that increases with time in any undisturbed ecosystem.[47]

Several measures of maturity are found in the ecological literature. These measures differ from one another in that some are structural and some are functional. Furthermore, some are used for comparing the state of maturity of climax communities in different environments and others are used for comparing the degree of maturity of communities in the same environment. In addition to measures of maturity there are measures for determining a representative or minimal area above which the community may be considered to increase merely in size. As Greig-Smith says, "the true characteristics of a plant community only appear when a certain minimal area of it is examined."[48]

Margalef uses a functional measure, the ratio of production to biomass (P/B), in his concern for the energy expenditure and efficiency of maintainance of ecosystems. "The relation," he says, "can be stated as flow of energy per unit biomass."[49] Mature ecosystems have a low P/B ratio and are more efficient. The reason for this is that:

> In ecosystems of higher complexity there is more complete use of food, there is a greater proportion of animals, and energy cascades through a more considerable number of steps. . . an ecosystem that has a complex structure . . . needs a lower amount of energy for maintaining such structure.[50]

Another very simple functional measure is Odum's production to respiration

---

47. Ramon Margalef, "On Certain Unifying Principles in Ecology," American Naturalist, XCVII (1963), p. 358.

48. P. Greig-Smith, Quantitative Plant Ecology (2d. ed.; London: Butterworths, 1964), p. 153.

49. Margalef, "Unifying Principles," p. 359.

50. Ibid., p. 360.

ratio (P/R). Odum is also concerned with energy but now with respect to the successional tendency to equilibrium. Thus, mature communities have P/R ratios of approximately 1 and succession may be either autotrophic or heterotrophic according to whether the ratio is, respectively, initially greater or less than 1.[51]

These two functional measures illustrate the different comparative uses of maturity measures; the P/R ratio for comparing mature communities in different environments and the P/B ratio for comparing communities undergoing succession in the same environment. For the former Margalef points out, for example, that the P/B ratio is higher for terrestial communities than for aquatic communities.[52]

A common structural measure is the diversity index, which is often high for mature communities. This is often calculated as the "generic coefficient," the ratio of the number of species to the total number of individuals. Another structural measure is Margalef's biochemical diversity ratio, calculated as the ratio of yellow to green pigment (D_{430}/D_{665}, where D is the optical density).[53] Diversity measures of maturity should be used with care since it is possible to think of communities, such as the Beech-Maple forest, which are less diverse at the climax than at some earlier stage. Odum, for example, compares the distribution of birds in two forest successions and finds that in one succession bird diversity

---

51. Howard T. Odum, "Primary Production in Flowing Waters," Limnology and Oceanography, 1 (1956), 102-17.

52. Margalef, "Unifying Principles."

53. Ibid.

increases to the climax whereas in the other succession diversity is at a maximum at earlier forest stages.[54]

Diversity measures of the type treated above are based on the quantitative relations among community components. Other measures are distributional in character and are measured in any of three ways. The "species area curve" is a measure where the area is large when the derivative approaches zero for complex communities; the "minimal area" is used to "adequately represent" the community and is large for complex communities: and there are also measures of "pattern" (deviation from random distribution and measured by association among members of a species or between species) in which, according to Whitford, the intensity of pattern tends to decrease toward maturity.[55] The major use of these measures is in determining how large an area is required for an adequate representation of the community for purposes of distribution and classification. For example, Cain and Castro compare stands in a Panamanian forest by using the species area curve.[56]

Conceptions of the community in terms of its parts.

Part I of this paper described the diverse kinds of material parts into which communities are analyzed. Briefly we showed that the kind of part depends, to a certain extent, upon the kind of problem. Some of the parts are species, pairs of species, synusia, associations, ecotypes, trophic

---

54. Eugene P. Odum, "Bird Populations of the Highlands (North Carolina) Plateau in Relation to Plant Succession and Avian Invasion," Ecology, XXXI (1950), 587-605.

55. P.B. Whitford, "Distribution of Woodland Plants in Relation to Successional and Clonal Growth," Ecology, XXX (1949), 199-208.

56. S. A. Cain and D. Castro, Manual of Vegetation Analysis (New York: Harper and Rowe, 1959).

levels and elements in a cycle.[57] Accordingly, there are different conceptions of the material organization of communities. Thus, one view treats community organization as a matter of the horizontal and vertical distribution patterns of its component species or groups of species; another view emphasizes the distribution of geographically defined communities; another view emphasizes the relationship among food and energy parts; another view emphasizes intraspecies adaptive units; and still another view emphasizes the relations among elements in a cycle.

The degree to which research papers are structural or functional in focus varies for these material conceptions of community organization. The first two views are based upon the spatial relations among community components, just as a city planner might describe a city in terms of the location of different ethnic groups. Accordingly, research with a structural focus is common with problems of this type, namely, in distribution, classification and nutrition problems. Of course, papers with a functional focus occur. Cowles's successional approach to distribution is illustrative.[58] The next three views are based upon functional relations among community components. Thus, the energy parts imply a "what-nourishes-what" relationship; the genetic parts imply an "adaptive" relationship; and the cyclic elements imply a "translocation" relationship. Accordingly research with a functional focus is common with problems of this type, namely energetic, genecological and

---

57. Connelly, "Patterns: I", pp. 8-9.

58. H. C. Cowles, "The Succession Point of View in Floristics," Proceedings of the International Congress of Plant Sciences, I (1926), 687-91.

metabolism problems. Of course, these problems may be attacked with a structural focus. The common practice of constructing food pyramids is illustrative.

Community boundaries

A review of the literature indicates that the kind of thing that can play the role of community varies in two ways, distributionally and functionally. This variation is due, in part, to the fact that community boundaries are often extremely vague, a fact which is taken to the extreme in the "continuum" concept of vegetation distribution.[59] Distributional variation further varies according to vertical and horizontal dimensions. Horizontally the community becomes a geographical entity. The vertical is, of course, normally accompanied by a statement of the geographical community limits. The vertical is seen in the studies on synusia and in homeostasis studies of light intensity modification in communities.[60]

Geographically the criteria for bounding communities vary from biotic to environmental factors to combinations of both. One of the effects of this variation is that what is taken to be an appropriate community varies radically in size. For Clements an appropriate community is climatically controlled and amounts to a major continental area.[61] Braun adds a biotic criterion and for her an appropriate community is a vegetation type within

59. Connelly, "Patterns: I", pp. 25-32.

60. Ibid., pp. 35-40, and Below, p. 31.

61. Clements, Plant Succession and Indicators.

the larger continental area.[62] Olson reduces the size of an appropriate community still further in his emphasis on local microenvironmental variation. Thus, the ridge area of a dune and the valley area between dunes are seen as two different communities.[63]

Researches using a functional determination of an appropriate community are normally accompanied by a statement of the geographic community limits. The significance of functional determinations in the choice of community will be indicated later. A few instances, are cited here. Miller, for example, chooses as his appropriate community one which exhibits the nutrient cycle as determined by research on an individual and its immediate environment.[64] In energetic studies the appropriate community is one which contains a set of energy transfer units. Still another illustration is seen in Leopold's concern for conservation and his notion of minerals washing from land to sea.[65] Here an appropriate community is a system of land and its run-off waters. We now turn to the question of principles involved.

Research conceptions of communities as a whole

Structure-function

We earlier saw one line of structure-function research in classification in our treatment of Principle B.[66] Suffice it to say that research proceeds

---

62. E. Lucy Braun, "The Undifferentiated Deciduous Forest Climax and the Association-Segregate," Ecology, XVI (1935), 514-19.

63. Jerry Olson, "Rates of Succession and Soil Changes on Southern Lake Michigan Sand Dunes," Botanical Gazette, CXIX (1958), 125-70.

64. Miller, "Plant Nutrients."

65. Aldo Leopold, "Lakes in Relation to Terrestrial Life Patterns," A Symposium on Hydrobiology (Madison, Wis.: University of Wisconsin Press, 1941), pp. 17-22.

66. Connelly, "Patterns: I", pp. 29-34.

by an initial "primary survey" in which the community and its parts are circumscribed. This is followed by a floristic analysis and the identification of the community and its parts according to dominant species. Dominance is used to account for integration within a community part and between parts of the community. Thus, says Clements, the main set of community parts, the 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.[67]

For this line of research the material organization of communities is a matter of the distribution of communities and their associated parts. An appropriate community is defined geographically and is determined by the distribution and relative abundance of species components. For this approach to structure-function, the notion of each part contributing to the whole is replaced by the notion of a control of community organization by the dominant species. (The notion of a central control is also present in early instances of structure-function research in organism physiology, e.g., the tendency to seek an account of the complexities of endocrine function in terms of a "master gland.")

Another line of structure-function research is seen in studies on food relations in communities. This approach adopts Elton's assumption that the number of predator-prey links is small.[68] Research proceeds by

---

67. Clements, "Plant Succession," p. 128.

68. Charles Elton, Animal Ecology (1st ed.; New York: Macmillan, 1927).

identifying the links and measuring them--and the producers, herbivores and decomposers--quantitatively either in terms of numbers or biomass. At this point there are two possible approaches to the research.

In one approach, research focuses on the numbers and biomass data and proceeds to construct diagrams relating the various energy parts. An example of this is seen in Lindeman's "Seasonal Food-Cycle Dynamics in a Senescent Lake" where he constructs a diagram of "generalized lacustrine food-cycle relationships." [69] A related approach is seen in the construction of "pyramids of numbers" where the researcher divides the fauna into size classes and constructs frequency histograms. The partially justified assumption is that size relationships correspond to trophic relationships.

The second approach focuses on rates of transfer between trophic levels, on respiration and other energy losses, and on efficiency of energy utilization. Here research may stress a quantitative analysis of the flow of energy through the system or it may stress the efficiency of translocation. An illustrative paper which stresses flows is seen in a study by Teal, who presents an "energy flow diagram for Root Spring." Here, inputs to the system in the form of dead organic matter and losses due to respiration and outflow of organic matter are included along with the translocations among the trophic parts of the system.[70] By itself, the flow diagram represents a study in antecedent-consequent events. Teal's concern, however, is to

---

69. Raymond L. Lindeman, "Seasonal Food-Cycle Dynamics in a Senescent Lake," American Midland Naturalist, XXVII (1941), 636-73.

70. J. M. Teal, "Community Metabolism in a Temperate Cold Spring," Ecological Monographs, XXVII (1957), 283-302.

treat the flow in terms of the various contributions to the over-all energy balance of the system. As such this is a study in structure-function with a focus on function. An illustration of the emphasis on efficiency of translocation is seen in a paper by Slobodkin who says, "The slow conversion of this potential energy to kinetic energy permits ecological communities to survive."[71]

For the line of research illustrated by Lindeman, Teal and Slobodkin the material organization of communities is a matter of the functional relations among trophic parts and these to the whole. As Hutchinson remarks:

> . . . the final statement of the structure of a biocoenosis consists of pairs of numbers, one an integer determining the level, one a fraction determining the efficiency.[72]

According to this line of research, an appropriate community is one which contains a set of trophic levels from production to decomposition. The approach through biomass and numbers data represents a structural focus in enquiry and the approach through translocations represents a functional approach in enquiry. In both approaches the starting point for the research is function. The studies tend to the "formal-holistic" in that a basic pattern is assumed to be present.[73]

Still another structure-function approach is seen in the genecological literature. Research proceeds by characterizing the environmental variation across a major biotic type. Reciprocal transplant experiments are

---

71. L. B. Slobodkin, "Ecological Energy Relationships at the Population Level," American Naturalist, XCIV (1960), p. 216.

72. Evelyn Hutchinson, "Addendum," in Raymond L. Lindeman, "The Trophic-Dynamic Aspect of Ecology," Ecology, XXIII (1942), p. 225.

73. In his paper "What Do Scientists Do?" Schwab describes the formal-holistic form of principle. He says, "When the distinguishing character of the subject of interest is treated as capable of embodiment in any one of a variety of materials or sets of parts, the holistic principle becomes formal."

conducted for groups of species found together on different parts of the environmental range. This is done for several environmental factors such that the resulting ecotypes are seen as being the outcome of adaptation to combinations of factors. The account of this approach is based upon McMillan's "The Role of Ecotypic Variation in the Distribution of the Central Grassland of North America." McMillan finds that:

> These studies of ecotypic variation . . . indicate that a certain combination of species in two areas may result from different phenomena. Through natural selection in different areas, groupings of individuals referable to the same species represent fundamentally different communities.[74]

The function of the ecotype is to "allow an apparently uniform vegetation . . . to be elaborated over an obviously non-uniform habitat."[75] From the point of view of the community this results in the "creation of geographic continua made up of site climax communities which are self-maintaining."[76]

For McMillan, community organization is a matter of local groupings of ecotypes whose function is to allow a given community type to adapt to variable environments. An appropriate major community is geographically determined and is seen in terms of the continuity of a physiognomic type.[77] This approach to structure-function is one in which both the parts and their functions are determined in a single experimental operation.

Homeostasis

Two lines of homeostatic research on communities as a whole are found

---

74. McMillan, "Role of Ecotypic Variation," p. 305.

75. *Ibid.*, p. 286. 76. *Ibid.*, p. 305. 77. *Ibid.*, p. 285.

in the literature. The first line closely follows the method described earlier for organism physiology.[78] In one such ecological research the study proceeds by determining the level of control of the equilibrium factor in question. The factor is then quantitatively modified and the researcher looks for mechanisms of compensatory replenishment and withdrawal. For example, in their paper "Translocation of Phosphorus in a Trout Stream Ecosystem," Ball and Hooper spent three years determining the seasonal constancy of dissolved phosphorus over a length of stream. They released radioactive phosphorus at the head of the stream and plotted uptake curves in all the significant biota and abiota.[79] An example of how they interpret their data follows:

> . . . the steady state did not vary with space and time and a regulatory mechanism must exist and this is probably storage in the plants and solids capable of absorbing phosphorus.[80]

For Ball and Hooper the material organization of the community is a matter of the abiotic and biotic factors which together constitute the mechanism of control of phosphorus. Here an appropriate community is one which exhibits this control.

A different pattern which also closely follows the procedure used in organism physiology emphasizes the fact of control as an indication of the stability of the system and as a preliminary to other research. Odum, for example, in his paper, "Trophic Structure and Productivity of Silver Springs, Florida,"

---

78. Connelly, "Patterns: I", pp. 19-21.

79. Robert C. Ball and Frank F. Hooper, "Translocation of Phosphorus in a Trout Stream Ecosystem," in Radioecology, ed. by Vincent Schultz and Alfred W. Klement, Jr. (New York: Reinhold PUblishing Corporation, 1963; Washington, D.C.: American Institue of the Biological Sciences, (1963), 217-28.

80. Ibid., p. 219.

says that "If a steady state exists powerful new approaches and methods are possible."[81] Thus, in sections titled "Chemostatic Properties" and "Biostatic Properties," Odum describes the period of time over which he has established the constancy of various chemical and biological factors. Odum then proceeds to give a structure-function account of the energetic relations within the community and between the community and the environment.

The material organization of the community in Odum's paper is, from one point of view, a matter of a collection of homeostases. From another point of view it is a matter of trophic levels related functionally to the whole. An appropriate community is determined by the former and is one which exhibits homeostasis in its biotic and abiotic components. In this pattern of enquiry emphasis is on the fact of control rather than on its mechanism.

A second line of homeostatic research is derived from the notion of an "internal environment." This conception, borrowed from the organism, is replaced in ecology by the notion of "microenvironment." There are numerous studies which describe the degree and means by which the "macroenvironment" is modified by communities to produce the "microenvironment." Research may focus on the degree of modification in a factor, as is seen, for example, in Geiger's The Climate Near the Ground;[82] or it may focus on the biotic and abiotic determinants of the modification. Saeki, for example, reviews research on light intensity and sunflecks on forest floors for forests with patchy canopies.[83]

81. Howard T. Odum, "Trophic Structure and Productivity of Silver Springs, Florida," Ecological Monographs, XXVII (1957), 55-112.

82. R. Geiger, The Climate Near the Ground (4th ed.; Cambridge, Mass.: Harvard University Press, 1964).

83. Toshiro Saeki, "Light Relations in Plant Communities," cited by Evans, "Ecosystem as the Basic Unit," 79-94.

A major approach of this sort is found in the agronomy literature concerned with crop production. Research proceeds by determining the degree of modification of different factors for various parts of the community. Thus, light intensity or carbon dioxide curves are plotted from the surface to the floor of a crop or the soil fertility level is determined at various points from the soil surface to the root tips. The modification is related, often experimentally, to factors such as density, other species, leaf arrangement and height. Research commonly describes the development of the modifiers and the resulting change in degree of modification over a period of time, normally a growing season. Results are presented as a proportion of the factor prior to modification. An illustration of this approach is seen in Donald's "Competition for Light in Crops and Pastures." Donald grows a pasture grass and a legume together at equal densities and under two conditions of nitrogen fertilization. He then plots foliage and light intensity profiles. He finds that under high, but not low, nitrogen fertilization, the light intensity is so modified by the grass that the production of the clover is decreased.[84]

For this research the material organization of the community is a matter of the distribution of the modifying agents. An appropriate community is determined by the similarities in the modifiers. Researches such as these emphasize the development of mechanisms of control as against the character of the mechanism or the fact of control as such. The homeostasis notion of the maintenance of a given level of control gives way to the notion of

---

84. C. M. Donald, "Competition for Light in Crops and Pastures: Mechanisms in Biological Competition," Symposia of the Society for Experimental Biology, XV (1961), 282-313.

variation in the control depending on the location in the community. For example, light intensity may decrease from 100 per cent to 10 per cent of incident radiation from the surface to the floor of a crop.

Regulation

We now turn to studies on regulation--studies which carry the notion of homeostasis to a new limit, that of maintaining an entire pattern of organization rather than a single equilibrium factor. My review of the literature has not encountered any full scale regulatory studies on communities. At most, researches tend toward regulation as extremes of the antecedent-consequent approach. However, as we earlier saw,[85, 86] there are regulatory studies on parts treated in isolation.

One barely discernible line of regulatory research is derived from Jenny's conception of the ecosystem. Jenny analyzes the ecosystem into independent and dependent variables. The independent variables (available organism, parent material, topgraphy, climate) consist of those conditions which are so massive or otherwise difficult of alteration that they may be considered as constraining factors on the system. The dependent variables are those which are developed within these constraints; the organisms which come to constitute the community, the soil as modified by the developing community, the microrelief and the microclimate which arise by the developing community.[87] The condition of independence among the independent variables

---

85. Connelly, "Patterns: I", pp. 23-29.

86. Above, pp. 3-4 and pp. 8-9.

87. Hans Jenny, "Derivation of State Factor Equations of Soil and Ecosystems," Soil Science Society of America Proceedings, XXV (1961).

is assumed and this, along with the notion that time zero for the system is arbitrarily chosen, gives rise to what Major calls "A Functional Factorial Approach to Plant Ecology."[88]

In the "functional factorial approach," research proceeds by selecting for comparison communities which exhibit all but one variable as a constant. Environmental and biotic factors are measured and accounts are given in terms of the changing relationship between these factors and differences in the independent variables. He reports that the pocket compared with the ridge has a less severe microenvironment, higher water and nitrogen levels, greater depth of soil, less loss of organic matter and a different vegetation. These differences are related to each other and are dependent as a whole, on the processes initiated by the topographic differences.[89]

In this research community organization is a matter of the interrelated, dependent, community variables. An appropriate class of communities is determined by a particular set of independent variables. If the research stopped at the point of discovering the kinds of communities that develop under such a set of constraints the research would be a straightforward case of antecedence and consequence. What distinguishes these studies from this simpler procedure is that the researchers expect and find a reportory of different parts and processes under each set of constraining circumstances. To the extent that this repertory is central the research borders on the regulatory.

---

88. Jack Major, "A Functional Factorial Approach to Plant Ecology," Ecology, XXXII (1951), 392-412.

89. Olson, "Rates of Succession."

In another line of research which tends to the regulatory communities are seen as being composed of a mosaic of "site types" or local climaxes. Environment is treated as given and the local climaxes represent cooperative adaptations of species populations to the environment. An example of this approach is seen in Whittaker's "A Consideration of Climax Theory: The Climax as a Population and Pattern."[90] Whittaker recognizes, where appropriate, a "prevailing climax type"[91] composed of a coherent "pattern of populations, variously related to one another, corresponding to the pattern of environmental gradients."[92] Environmental gradients are identified and the association of species is determined by the usual counting and distance-between-individuals methods.

According to this view, community organization is a matter of the distribution of the site types, each of which is in adaptive harmony with the environment. An appropriate "climax type" is determined geographically by physiognomic characteristics of the vegetation.

This research is distinguished from antecedence and consequence in that stress is placed on the adaptation of site types to environment rather than treating the site types as mere products of environment. The research is, furthermore, distinguished from structure-function research in that an array of site types is treated as allowing the community to persist rather than emphasizing the particular function played by each site type. We may think of this research as regulatory in that there are as many interchangeable site types as there are different local environments and it is this variable array which maintains the community.

---

90. R.H. Whittaker, "A Consideration of Climax Theory: The Climax as a Population and Pattern," Ecological Monographs, XXIII (1953), 41-78.

91. Ibid., p. 59.

92. Ibid., p. 60.

In another line of research the notion of regulation is discernible as constituting a transition from homeostasis. Emphasis is placed on the limiting conditions beyond which the community, instead of maintaining itself, is transformed into another. Lindeman's paper "The Trophic Dynamic Aspect of Ecology" is illustrative. Lindeman describes the changing energy functions as a lake undergoes succession to a terrestrial forest. He describes an energy curve for this succession. The curve has a number of plateaus representing comparatively stable communities, for example, a peat bog stage.[93]

This approach to regulation is the basis for conservation pleas. A question, for example, which asks "how large a preserve is required for the preservation of a redwood forest" focuses on size as a limiting condition. The same emphasis is seen in the treatment of Lake Michigan as undergoing an enrichment process in which producers flourish, diversity decreases and the lake enters a new immature phase.

According to this approach, community organization is, at one level, a matter of a sequence of relatively stable morphological types. Underlying the apparently stable morphology, community organization is a matter of processes of change in the microenvironment. This is an approach in which there may be a virtually unlimited morphological and functional repertory. Conditions of stability exist for each morphological type. Functional stability, however, is a question of relative rates of change and there are, correspondingly, only rate-reducing conditions of functional existance.

---

93. Lindeman, "The Trophic Dynamic Aspect of Ecology," American Midland Naturalist, XXIII (1942).

Very little regulatory research is done of the sort illustrated by Lindeman and our comments on Lake Michigan. Nevertheless, the conceptual importance of enquiry into the conditions of stability and change in apparently stable states is recognized. Witness, for example, Slobodkin's remark that:

> The future development of theoretical community ecology will probably be based on considerations of community stability. It is known that any ecological change will shift the entire community to a new stable state, although the theory of these stable states has not yet been formulated.[94]

Another wide range of problems is treated in terms of cycles. Thus, there are "circadian cycles," annual cycles, production cycles, reproduction cycles, local nutrient cycles, environmental cycles, population numbers cycles, cycles of succession in nature communities and food cycles. Two main approaches to cycles are found in the literature: the study of the periodic appearance of a part or event, and the study of the translocation of something.

Studies in periodicity may assume a correlation between the appearance of an event and a cycle in the environment. In this case the event is treated as representing an adaptation to the environmental cycle. Periodicity studies may, instead, assume a correlation between the event and the biological properties of species or species interactions. Most problems may take either of these assumptions as their starting point. Thus there is Elton's (now largely abandoned) "sun-spot theory" of population cycles[95] and Nicholson's "predator-prey theory" of population cycles.[96]

---

94. Slobodkin, Growth and Regulation, p. 171.

95. Charles Elton, "Periodic Fluctuations in the Numbers of Animals: Their Causes and Effects," Journal of Experimental Biology, II (1924), 119-63.

96. A.J. Nicholson, "The Self Adjustment of Populations to Change," Cold Spring Harbor Symposium in Quantitive Biology, XXII (1957),

Studies on cycles may simply describe the events in the cycle or, perhaps, they may examine the various links in the cycle in terms of one stage or event giving rise to a next stage or event. Godwin and Conway's account of cyclic succession illustrates this typically antecedent-consequent approach.[97] Homeostasis approaches to nutrient cycling are also common and are illustrated above.[98] Other studies tend to the regulatory. In such studies research proceeds by identifying the period of appearance of the event. Next, the intervening events are described. In the case of an assumed control by environment, the researcher looks for cyclic factors in the environment. In the case of an assumed biotic control, the researcher looks for a controlling interaction such as competition or dominance. An illustrative case of the latter is Watt's "Pattern and Process in the Plant Community." Watt describes a cyclic succession of species in a nature community. He attributes the cycle to the decreasing level of dominance with age of the dominant species.[99]

In the cyclic approach to regulation, community organization is a matter of a cycle of morphological changes associated with a cycle in function. An appropriate community is one which maintains a morphological constancy by the cyclic succession of its parts. As Watt remarks:

> Although there is change in time at any one place, the whole community remains essentially the same; the thing that persists unchanged is the process and its manifestation in the sequence of phases.[100]

This is a study in regulation in which the community is preserved by continuous cyclic changes of its parts.

---

97. Godwin and Conway, "The Ecology of a Raised Bog," Journal of Ecology, XXVIX (1939).

98. Above, p. 5 and p. 8.

99. Watt, "Pattern and Process."

100. *Ibid*., p. 3.

A SUMMARIZED ACCOUNT OF THE PATTERNS OF ENQUIRY

The four principles of biology are specified to ecology, with two exceptions, in each of the five problem areas giving eighteen significantly different patterns of enquiry. These patterns are summarized below in terms of conception of community, required data, and interpretation to the form of a statement of outcomes.

Antecedent-Consequent

Classification and taxomony

Here, communities are treated either in terms of the overlapping distributions of their component species with respect to environmental differences or in terms of the coassociation of their component species. In the first case data are collected on the distribution of species relative to environmental differences and gradients. In the second case data are collected on the presence or absence of species or on the coassociation of species as determined, for instance, by distance-between-individuals techniques.

Classes are constructed on the basis of similarities between species with respect to either type of data. The resulting classification is thought of as being "arbitrary" and "objective."

Energetics

Communities are treated in terms of assemblages of producing individuals responding to independent factors in the environment or in terms of networks of individuals connected by their trophic habits.
Data are collected on a measure of production such as biomass in relation to an environmental factor or, in the second case, on what-nourishes-what by such techniques as direct observation, stomach analysis or isotope tracer.

In the first case variation in production is treated as being dependent on variation in the environmental factor. In the second case data are used to construct links, chains and webs of food relations and, thereby, a step by step account of energy flow through the community.

Nutrition and metabolism

The community is treated in terms of the requirements of its component species or in terms of nutrient cycles. In the first case data are collected on the environmental conditions associated with the successful maintenance of a species. In its most simple form this amounts to data on the local distribuiton of individuals with respect to local variation in a single environmental factor or on the growth response of individuals under controlled conditions of variation with respect to the factor. At its most complex this amounts to describing the environment throughout the life cycle of the species, or through a cycle of seasons. In the second case data are collected on the content of an element in various parts of a plant and its immediate environment.

Fór the first case, the data amount to a description of the physiological requirements of the species. In the second case, data are connected to form a cycle of events for a nutritional element.

Genecology

Communities are treated in terms of the genetic variations of their component species with respect to gradients in environmental factors. First, data are collected on the phenotypic variation of a species with respect to environmental differences. Next, using transplant techniques, data are collected on the form of the organisms grown under different conditions along the environmental gradient.

The genotypic variation, distinguished from environmental plasticity by the transplant data, is assumed to have arisen as an effect of the differential selective effect of the environmental gradient. Species ecoclines are thereby formed and described by the research.

Distribution

Here the conception of the community is the same as that described for Classification. The same kinds of data are collected by the same techniques.

The data are used to give comparative accounts of the tolerance limits of species and, by the use of one or another distributional equation -- e.g., binomial, Poisson -- accounts of the distributional form.

Structure-Function

Classification and taxonomy

Here the community is conceived in terms of a set of "association" parts, identified by their dominant species functionally associated with one another and with the whole community. Communities and their associations are tentatively described by an initial survey. Data are collected on the overlapping distributions of dominant species and, where communities do not fit the developing classification, on environmental conditions.

Communities are classified and food habits are used to construct a trophic level structure of the community. Each of the levels is seen as contributing to the over-all energy balance and efficiency of the community as determined by the data on metabolism.

Nutrition and metabolism

I have not found any nutrition and metabolism papers dealing with particular communities. However, there are papers whose aim is to develop a structure-function conception of the nutritional relations of communities.

For example, land, lakes, and organisms may be treated as forming three parts of a landscape whole. Minerals wash to lower levels through the influence of gravity. The function of lakes and soils is to retard this flow. Organisms serve to reverse the flow via their "pumping" action from the soil and air through the food chain network. Together these parts and their functions constitute a nutrient cycle which allows for the continued existence of organisms on land.

Genecology

Here the community is treated in terms of the genetic adaptation of groups of organisms within a species to differences in environment. Data are collected on the association of species and on the phenotypic variability of each of these species over a range of environments within a physiognomically determined community type. Transplant experiments are conducted on members of the species from different parts of the environment and the resulting ecotypes are characterized according to that aspect of the environment to which they are adapted.

The data are used to describe the parts of the community in terms of the similarities in ecotype adaptation for different species. As a whole the ecotypes allow a relatively uniform community type to persist over a variable environment.

Distribution

Here the community is treated in terms of the numbers and kinds of organisms it will maintain as a function of its niche diversity. ("Niche" is a functional term expressing the way a species uses its habitat). Data are first collected on species distribution and abundance. For closely related species occupying the same habitat morphological and behavioral data are now collected.

Since it is assumed that no two species can occupy the same niche the first set of data is used as evidence of niche diversity. Comparisons between species with respect to the second set of data are evidence of the particular function involved.

Homeostasis

Classification and taxonomy

I have not found any papers in this area although it is possible to conceive of classifications based on the homeostatic criteria of controlled factors, levels of control and mechanisms of control. It is known, for example, that in the arctic population numbers and available nutrients undergo comparatively wide fluctuations in time. This suggests the possibility of classifying communities according to the form of their population numbers curve plotted against time.

Energetics

Here the community is treated in terms of its productivity as limited by mechanisms of control over factors (e.g. light) influencing production. Data are collected on productivity, on the level of a community factor according to different parts of the community, and on the modifiers (e.g. density, leaf arrangement) of the factor.

Data on the limiting factor are presented as a proportion of the factor prior to modification by the community. The modifiers and their influence on the factor influencing production amount to the mechanism of homeostatic control.

Nutrition and metabolism

Here the community is treated in terms of the control of available nutrients by cycles of nutrients in the community. The same data are collected as described for the antecedent-consequent approach to cycles. The various parts of the cycle are seen as maintaining a relatively constant level of available nutrient.

Genecology

Here the community is seen in terms of the stability of ecotypes and their associated genomes. Data are collected on the number and coassociation of genes by techniques of ecotype crossbreeding.

Ecotypic stability is attributed to the transmission of arrays of genes from generation to generation. The array of genes, along with measures of their association amounts to the mechanism of control. (This pattern of research depends on a prior determination of the existence of ecotypes).

Distribution

Here the community is seen in terms of the mechanisms of control of population numbers. Data are collected on the fluctuations of numbers and on related environmental conditions, including other species.

The fact of control is established on the basis of the ability to show that the fluctuations in numbers exhibit a reasonably constant average through time. The various associations of the environment with the numbers fluctuation amounts to the mechanisms of control.

Regulation

Classification and taxonomy

I was unable to find any papers in this area.

Energetics

I find papers in which the conception of regulation is expounded and some in which it is asserted to be the governing concern of the reported resea-ch. However, none of the papers do, in fact, collect and interpret data so as to exhibit actual regulatory energetic processes in communities. There are, however, descriptions of the community as a kind of prototype of a regulatory system. Such descriptions are made in terms of inputs, outputs and translocation of energy but on the whole such descriptions constitute little more than a complex antecedent-consequent account.

Nutrition and metabolism

The open system conception described for energetics applies but now with respect to minerals. Data are collected on variables which are dependent on the community and on the independent variables.

The research looks for and finds a repertory of relations between different nutrients and between these and vegetation.

Genecology

I have not found any regulatory approaches to the genecology of communities. However, there are theoretical regulatory accounts for species. For example, a genetic system may be treated in terms of a set of variables related in such a way that a change in any one has its effects on all the others. The classes of variables are the mating system, breeding system, phenotypes, genotypes, karyotypes and distribution patterns. The system as a whole is capable of a variety of states of existence as defined by the set of these variables.

Distribution

The community is seen in terms of a repertory of distribution patterns. Data are collected on the distribution of species with respect to the environment or with respect to other species through time.

The first set of data is used to give an account of the community in terms of a repertory of distribution patterns with respect to environmental variation. In the second case the repertory is in respect to regular changes in the distributional relations among species through time such that the whole community but no one part of it remains stable.