A History of the Ecosystem Concept in Ecology

More Than the Sum of the Parts

Frank Benjamin Golley

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ABBREVIATIONS

AEC	Atomic Energy Commission
BES	British Ecological Society
CNRS	Centre National de la Recherché Scientifique
EDFB	Eastern Deciduous Forest Biome project
ELM	Grassland system model
ENCORE	European network of catchments for ecological research
FAO	Food and Agriculture Organization
IBP	International Biological Program
ICSU	International Council of Scientific Unions
IGY	International Geophysical Year
IUBS	Union of Biological Sciences
IUCN	International Union for the Conservation of Nature
MAB	Man and the Biosphere program
MEDECO	Mediterranean Ecological Society
NAS	National Academy of Science
NSF	National Science Foundation
PERT	program evaluation and review technique *(sys. eng.)*
RANN	Research Applied to National Needs
RES	Regional Environmental Systems
SIL	*Societas Internationalis Limnologiae Theoreticae et Applicatae*

SREL	Savannah River Ecology Laboratory
UNESCO	United Nations Educational, Scientific, and Cultural Organization
WHO	World Health Organization

CHAPTER 2

The Genesis of a Concept

In 1935 Alfred George Tansley (1871–1955) introduced a new word to the world. *Ecosystem* referred to a holistic and integrative ecological concept that combined living organisms and the physical environment into a system. Tansley presented the ecosystem concept in a twenty-three-page article titled, "The Use and Abuse of Vegetational Concepts and Terms" in the scientific magazine *Ecology:*

> But the more fundamental conception is, as it seems to me, the whole *system* (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense.
>
> It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth.
>
> These *ecosystems,* as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom. (Tansley, 1935, 299)

Thus, Tansley's ecosystem concept identified a system that was: (l) an element in a hierarchy of physical systems from the universe to the atom, (2) the basic system of ecology, and (3) composed of both the organism-complex and

the physical-environmental complex. From this origin in 1935 to the present, Tansley's ecosystem has remained a key concept in the ecological sciences.

TANSLEY THE MAN

Certainly the success of the ecosystem concept was partly due to the distinguished reputation of its creator. Arthur George Tansley was born in 1871 in London, the only son of a businessman, George Tansley, who had retired at an early age to give his time to voluntary teaching and public work. Arthur George Tansley was attracted to the study of field botany and entered the University of London to attend lectures in the biological sciences before completing his preparatory studies. He went to Trinity College, Cambridge, in 1890, where he read botany, zoology, physiology, and, in the last year, geology. He received a first class in part 1 of the Cambridge Natural Science Tripos, whereupon he returned to University College, London. There he served as assistant to the distinguished botanist F. W. Oliver. Tansley stayed in London until 1906, during which time he repeated his performance in the second part of the Cambridge Natural Science Tripos. He then returned to Cambridge as a lecturer at the Cambridge Botany School under Prof. A. C. Seward.[1]

Although Tansley began his scientific work as an anatomist, he was directed toward plant ecology through his early interest in field botany. Later, as a trained scientist, he was influenced by a trip he made to Ceylon and the Malaya Peninsula in 1900/01 and by Oliver's interest in field studies of maritime communities. He had initiated the scientific journal *The New Phytologist* in 1902, which he edited for thirty years (1902–31). Through this journal Tansley was able to provide an avenue for research that did not fit the conservative standards of the botanical journals. This research included ecological studies. In 1904 he called for establishment of a vegetation survey of the British Isles, and in 1912, when this survey had lost its momentum, he worked to form an association of ecologists. In 1913 the first ecological society in the world was organized, with Tansley as its president. He was made a fellow of the Royal Society in 1915 and appointed to the Sherardian Chair of Botany in Oxford in 1927 (fig. 2.1), in which position he served until his retirement in 1937. He was knighted in 1950.

The biological details of Alfred George Tansley suggest that he was not only an acknowledged leader of British plant ecology but that he achieved substantial personal success as a result. Actually, the situation was quite different. Tansley struggled throughout his career to open traditional botany to ecology and to have ecology equally accepted as part of the natural sciences. His

2.1 Painting of Sir Arthur George Tansley when he served as professor of botany, Oxford University. Reproduced with permission of the President and Fellows of Magdalen College, Oxford

commitment to service in his profession, together with tolerance and persistence, eventually led to success. His professional advancement was delayed, however, and the frustration this delay caused must have been intense.[2] In 1912 he contemplated moving to an academic post in Australia, and in 1922—partly from his concern for first world war veterans suffering mental problems from trench warfare and partly from his frustration with academic life—he visited Sigmund Freud in Vienna to further his study of psychology. The following year he resigned his lectureship and moved his family to Vienna to study with Freud[3] and initiated a practice in psychology when he returned to Cambridge. Although his practice was soon abandoned, his textbook *The New Psychology and Its Relation to Life,* was successful and was reprinted and translated several times.

Arthur Tansley was a highly motivated, effective leader for ecologists, with a deep interest in philosophy and psychology, personally familiar with the pioneers of ecology in other countries, and a scientist with exceptionally high standards. Chiefly through his work as an editor, Tansley set a standard for

ecological science, and it was from his complex personality that the ecosystem concept emerged.

Terms and Concepts of Vegetation

Tansley's article on vegetational terms and concepts was an invited contribution for a festschrift for another ecologist, Henry Chandler Cowles (1869–1939). Cowles was associated with the University of Chicago and at the turn of the century carried out a series of studies on plant succession on the sand dunes of Lake Michigan, as well as other habitats in the Chicago area (Cowles, 1899, 1901). Tansley offered his article as a contribution to a subject in which Cowles had special interest. He honored Cowles by saying, "During the first decade of this century indeed Cowles did far more than any one else to create and to increase our knowledge of succession and to deduce its general laws."[4]

The immediate stimulation for the subject of the treatise on vegetational terms and concepts, however, was, according to Tansley, the appearance of four articles by the South African ecologist John Phillips,[5] which concerned the biotic community, succession, development, the climax, and the complex organism (Phillips, 1931, 1934, 1935a, 1935b). In these articles on succession and community organization Phillips related the concepts of the American ecologist Frederic Clements (1874–1945) to philosophical concepts of the biotic community as a complex organism and as a philosophical whole, after the ideas of Jan Christian Smuts (1870–1950). Phillips (1931) devoted most of his first treatise on the biotic community to his argument that ecologists should consider both plants and animals as members of a biotic community. Reading before the 1930 International Botanical Congress, Cambridge, he emphasized the place of animals in the organization and structure of communities.

> When elephant [sic] frequent any portion of forest for any length of time, they are invariably followed by the scavenging *Potamochoerus choeropotamus* (wild pig), and at times by baboon, which take advantage of the roots and bulbs displaced by the great animals, and which are not above searching the droppings for food. The disturbance to the soil caused by the elephant, the wild pig and the baboon, brings about soil improvement, and stimulates many dormant seeds to germinate. Fruits passed through the animals are cleaned of their outer coverings and fall into improved germinating beds. Naturally a certain proportion of the fruits is spoilt in the process of passing through the animals, while existing regeneration may be destroyed. (Phillips, 1931, 11)

Because ecologists tended to restrict their attention to plants or animals exclusively, Phillips was reiterating an important point made earlier by A. G. Vestal (Illinois plant ecologist) (1914), Frederic Clements (1916), and Victor Shelford, animal ecologist at the University of Illinois (1926).It was only in his conclusion that Phillips departed from the evidence:

> It is in keeping with the importance of the subject that I should at this juncture refer to a further aspect of the community—that aspect that has already called for criticism from certain quarters—the community as a *complex organism.* Clements (8, p. 199; 10, p. 3; 16, p. 314) in his purpose of introducing the term and view appears to have been misunderstood by some (18, 24), but has had the support of Tansley (41, p. 123; 43, p. 678), provided the term *quasi*-organism is employed and provided the concept applies to Tansley's *autogenic* succession. Briefly Clement's purpose is to emphasize the organic entity of the community, his epithet *complex* immediately distinguishing this *communal* organism from the *individual* organism of general terminology. While I—and doubtless Clements himself—would agree that philosophically General Smuts (40, pp. 339–43) by his masterly and inspiring exposition—in a universal connection—that groups, societies, nations, and Nature are *organic without being organisms,* are holistic without being wholes—has pointed to the truth, I still am able to see that the concept of the *complex organism* has much to commend it in practice. It certainly focuses attention—and such a focussing is essential to advance—upon the place and function of all life in that organic entity the community.
>
> A biotic community in many respects behaves as a complex organism—in its origin, growth, development, common response, common reaction, and its reproduction. In accordance with the holistic concept of Smuts (1926), the biotic community is something more than the mere sum of its parts; it possesses a special identity—it is indeed a mass-entity with a destiny peculiar to itself.[6]

Phillips's other three articles each presented an aspect of a single argument and expanded upon his ideas (Phillips, 1934, 1935a, 1935b). His purpose was "a careful review of the highly polemical field concerned with the essential nature and the direction of *succession* and *development*; the nature of the *climax*; the existence of the *complex organism*; and the inherent oneness of the *complex organism* and the *biotic community*" (Phillips, 1934, 555). Phillips's technique in these articles was to pose a series of questions concerning the many possible interpretations of a concept, review the literature—showing how various ecologists addressed the questions—and then to draw his own conclusions. He derived his answers apparently entirely arbitrarily, but with reference to the authority of Clements, Smuts, Tansley, and others.

Clements

more than sum of parts

The intellectual idea Phillips was advancing in his articles affected a major topic of ecological discussion and argument: the nature of the biotic community. The creative element in Phillips's writings was the connection of the thought of Clements and Smuts in defense of Clements's concept of the community as a complex organism. In the first part of a three-part series, Phillips concluded, with Clements, that ecological succession is always the result of biotic reactions on the environment and that it is always progressive. That is, succession is convergence toward an end-point, called the climax community, and it represents a process of development of a complex organism.

In his second treatise he dealt with two aspects of the Clementsian paradigm. First, he asserted that the process of development causes integration to occur among the biota within the community. Second, the climatic climax is set by the regional climate, and there is ideally only a single climax (the monoclimax) in a region. That is, the climax community is in a dynamic equilibrium with the climax habitat, but this equilibrium is not static or permanent.

Phillips's final treatise was a philosophical defense of the concepts of emergence and the complex organism. Phillips thought that emergence "appears to offer [the ecologist] a vantage point from which to survey characteristics of novelty, of integration, of wholeness, emergent from succession and development in biotic communities. . . . Communities are not mere summations of individual organisms, but are integrated wholes with particular emergents" (Phillips, 1935b, 490).

Phillips did not present new evidence for these community concepts. Rather, he was reviewing the arguments about the origin and character of ecological communities and defending the Clementsian position. Part of his strategy in these articles was to appeal to an authority to make his argument more convincing. Frederic Clements was an authority figure in American ecology, and his theories of plant succession and the nature of the community were widely accepted by American ecologists. According to Phillips, Clements provided the most inclusive explanation of these phenomena. Jan Christian Smuts was the prime minister of South Africa and an authority figure for Phillips. In turn, Phillips also involved Tansley, the most distinguished British ecologist, as a further but more tangential authority for his integrating treatises.

The relation between Phillips, Clements, Smuts, and Tansley is complex. Phillips was younger than the other three. He was personally acquainted with Clements, having visited him in America. He was attracted to Clements's ideas, had introduced Smuts's ideas to Clements, and became an advocate of Clementsian ecology in Africa. Phillips was also personally connected with Smuts,

2.2 Participants in the International Phytogeographical Excursion, in England, 1911. Seated on the ground, left to right: T. W. Woodhead, C. E. Moss, Frederic Clements, Weiss; seated are G. C. Druce, Mrs. Tansley, unidentified woman. Standing: unknown, J. Massart, C. Schroter, C. H. Ostenfield, Arthur Tansley, unknown, H. J. Cowles, L. A. Rubel, O. Drude, unknown, Mrs. Cowles, unknown, unknown, W. G. Smith, unknown, C. A. M. Lindeman. Individuals identified by John Sheail (Sheail, 1987). Photograph courtesy of the Clements Collection, American Heritage Center, University of Wyoming

having been part of a circle of younger men around the general. Phillips was not, however, personally acquainted with Tansley. He did know that Tansley and Clements were professional friends who had become acquainted through the International Phytogeographical Excursions of 1911 and 1913 that had taken place in England and North America (figs. 2.2 and 2.3) and that they and their wives corresponded regularly. Although Tansley accepted some of Clements's interpretations of vegetation patterns and introduced and used them in his work on British vegetation, he distanced himself from Clements's more extreme interpretations of the community as a complex organism and as a developing organism through ecological succession. Tansley made an attempt to accommodate Clements, but he was philosophically opposed to extreme speculation and arid intellectual taxonomy. Phillips would have done well to leave Tansley out of his pantheon of authorities.

2.3 Participants of the International Phytogeographical Excursion, in Yosemite, California, 1913. Seated, left to right: J. Massart, Arthur Tansley, Fisher, L. A. Rubel, behind, Skottesberg. Standing: unknown, Mrs. Tansley, Mrs. Brockman-Jerosch, H. J. Cowles, C. Schroter, Engler, Edith Clements, with Frederic Clements (with hat) behind them. Others unknown. Photograph courtesy of the Clements Collection, American Heritage Center, University of Wyoming

Clearly, Tansley was offended by Phillips's articles. He was motivated to write *Use and Abuse of Vegetation Concepts and Terms* for the ecological community partly for scientific reasons concerned with the nature of the evidence and partly from the need to defend ecology from a too extreme philosophizing and to maintain its connection to mechanistic, reductionistic science and therefore its reputation within biology. In fulfilling this latter objective, Tansley's senses were sharpened by his personal difficulty in establishing ecology as a respectable discipline. Tansley was also put off by Phillips's mode of presentation, which seemed analytical but was actually quite arbitrary. We can understand how his statements caused Tansley to imply that they represented a closed system of religious or philosophical dogma. Tansley commented in an uncharacteristically harsh manner: "Clements appears as the major prophet and Phillips as the chief apostle, with the true apostolic fervor in abundant measure."[7] Even though "the *odium theologicum* is entirely absent," he wrote, "indeed the views of opponents are set out most fully and fairly, and the heresiarchs, and even the infidels, are treated with perfect courtesy" (Tansley, 1926, 677). Thus, Tansley's impatience with Phillips's articles probably stemmed as much from their underlying philosophical structure, which seemed to shape Phillips's presentation, as from their scientific content.

Although Tansley's article was concerned mainly with the terms and concepts reviewed by Phillips—succession, development and the quasi-organism, climaxes, the complex organism, and biotic factors—the new idea he offered was the ecosystem. In his presentation of the ecosystem concept, Tansley emphasized its physical character and its relation to physical systems in general. He made a decided effort to avoid biological metaphors and analogies. Although he stressed that ecosystems involved the interaction of the biota (he used the term *biome*) and the environment, he also placed the ecosystem within a larger ecological context. This larger context was the *formation*, usually defined as the regional vegetation adjusted to broad soil and climate patterns. Tansley used the formation to represent the climate, which he said contributed parts or components to the system together with the soil and organisms. Finally, the ecosystem concept he presented was part of several discussions of physical and ecological equilibrium.

Probably Tansley's use of equilibrium would be most problematic to today's ecologist. His concept of dynamic equilibrium has several elements. First, systems closer to equilibrium are most likely to survive. Second, equilibrium develops slowly as systems become more highly integrated and adjusted. The climax represents the nearest approach to a "perfect dynamic equilibrium" possible to obtain under the given conditions. Third, the equilibrium is never perfect; its perfection is measured by its stability. Compared to chemical systems, ecosystems are not stable because of their unstable components of soil, climate, and organisms and also because they are vulnerable to invasion by components of other systems. Finally, while it is possible that there is continual change in the system components, Tansley counsels us to split up the process of change and focus on the phases that are dependent upon the processes involved. Thus, Tansley's ecosystem concept is a physical concept, based on the concept of equilibrium and emphasizing the interaction of physical-chemical and biological components.

Tansley's offering to the Cowles festschrift was designed to be an analysis of ecological language leading to a new alternative that would maintain ecology's links with the modern physical sciences and also create further bridges between alternative ecological approaches. His strategy was to address a variety of conceptual problems concerned with the nature of ecological communities and the consequences of speculative thinking in ecology.

THE ECOLOGICAL CONTEXT OF THE TANSLEY TREATISE

For at least a hundred years before the Phillips-Tansley exchange took place, field ecologists had been observing the patterns of organisms in nature and trying to understand how these patterns were formed and maintained by the interaction of the biota with the physical environment. The history of the development of ecological community concepts is one contextual element of the exchange. Tansley had been active in this type of research. He had organized the survey of British vegetation in the first decade of this century and had written *Types of British Vegetation* in 1911. In his response to Phillips and in his analysis of vegetation terms he was speaking from deep experience.

Depending upon the focus and scale of observation, the ecologist examining the patterns of vegetation might see an individual organism, a population of individuals, or aggregations of organisms in the form of forests, fields, and coastal banks. It was commonplace for nonscientists to recognize that nature was organized into forests, meadows, bogs, lakes, and so on. The early ecologists who focused on these commonplace units of nature usually presented their findings as lists of the species made up the biota of the unit, using the methods of Linnaean taxonomy. Ecological observation led to establishing lists of the species encountered on the survey. Ecologists then speculated about why particular species were present or absent, or why they were represented abundantly or rarely.

There are many examples of this early type of vegetation analysis, but the delightful report of Anton Kerner von Marilaun (1831–98), professor of botany at the University of Vienna, of his mid-century travels through the Danube Basin (1863) conveys especially well the character of these writings. In the following extract Kerner is thinking about the reasons why organisms are aggregated into communities:

> Wherever the reign of nature is not disturbed by human interference the different plant-species join together in communities, each of which has a characteristic form, and constitutes a feature in the landscape of which it is a part. These communities are distributed and grouped together in a great variety of ways, and, like the lines on a man's face, they give a particular impress to the land where they grow. The species of which a community is composed may belong to the most widely different natural groups of plants. The reason for their living together does not lie in their being of common origin, but in the nature of the habitat. They are forced into companionship not by any affinity to one another but by the fact that their vital necessities are the same. It may perhaps be true that

> amongst the many thousands of plants inhabiting the earth no two are to be found which are completely alike in their requirements in respect of the intensity and duration of solar illumination, the concurrence of a particular duration of daylight with a certain amount of heat, the composition and quantity of the nutrient salts available at the places where the plants live, the amount of moisture in the air and in the ground, or, lastly, the character of the rainfall. This does not, however, exclude the possibility that in particular places similar demands may be met, and that different species with similar needs may flourish undisturbed side by side as men live together in one house or in one town, and, although their customs and their needs may not be exactly the same, yet form a society which is permanent and thrives, and wherein each member feels at home, because it rests upon common usages and is adapted to the local conditions. Nor is it impossible that each one may derive an advantage from the common life, that the associated individuals may support one another in the conduct of their lives, and that they may even be dependent upon one another. (Kerner, 1897, 885)

Kerner's interpretation of his observations introduce several important features of the genre. First, Kerner has focused on the plants in the passage quoted. This focus is evidence that ecologists were trained as plant or animal biologists and therefore tended to study plants or animals exclusively. Although partly owing to their training in separate disciplines in biology, this forced separation was due to the difficulty of mastering the taxonomy of several groups of organisms. As Phillips emphasized, before nature could be studied as a system it was necessary that all the parts be included.

Second, Kerner interpreted these groupings of plants to be communities, thinking analogically from human communities. In the writings of many authors at this time nature was being interpreted through the metaphor of a human community. Kerner was using the community metaphor in its positive, almost idyllic form, ignoring the reality of the human community in which he lived. At this particular time Europe was undergoing rapid social change as a result of industrialization, urbanization, and intense nationalism. In reaction, there was an emphasis on traditional, idealistic community forms and values, especially in the German romantic tradition, and these forms and values probably underlay Kerner's use of the metaphor. Social Darwinism and the human state interpreted as continual warfare was to come later.

Third, Kerner advanced two explanations for community formation. On one side, the community may be formed by a joint interchange and interaction between coexisting individuals. The community grows out of cooperation and

competition between individual organisms. On the other side, they may be forced into companionship not by any affinity but by their joint needs, which are met in that particular habitat.

At the time of Kerner, ecological investigation was almost entirely observational. The ecologist walked or rode across a community and observed the presence, absence, and abundance of various organisms and interpreted those patterns. By the end of the century, however, ecologists were beginning to use quantitative methods in their investigations. For example, at the University of Nebraska, Roscoe Pound, later to be a famous jurist, and Clements applied a standard method of data collection derived from methods used by the German plant ecologist Oscar Drude and reported in his book *Deutschlands Pflanzengeographie*. Pond and Clements used square quadrats, five meters on a side, to define a limited plot of ground and recorded the frequency and abundance of individuals in those areas. By taking data from many quadrats within a community, they were able to observe variations in plant composition that were not visible to the naked eye and create quantitatively defined ecological units.

The ecologist using quantitative methods might conclude that the ecological units defined so precisely were concrete and fixed. Pound and Clements in their report on the phytogeography of Nebraska expressed this opinion:

> The vegetation of the earth's surface is arranged into groups of definite constitution and of more or less definite limits. Such a group is a plant formation. It is necessary to distinguish very carefully between formations and minor groups, facies, and mere patches. A formation is invariably a plant-complex, except in its incipience or decadence. It has to do primarily with the species which compose it, though these are represented in it necessarily by individuals, while a facies or a patch derives its character solely from the individuals of its species. . . . The plant formation determines not only the constitution of the floral covering, but is also a more or less interpretable expression of those biological forces of which it is a resultant. It is a biological community in which each factor has more or less interrelation with every other factor, a relation determined not merely, nor necessarily, by the fact of association but also as a result of biological forces induced by physiographical and meteorological phenomena. (Pound and Clements, 1897, 313–14)

In Pound and Clements's explanation of the patterns of plant distribution, they mention the role of both biotic interaction and the physical environment. Later, these factors became transformed in the Clementsian theory of development of the complex organism. As Phillips stated, the climate set the type of the climax vegetation, while development was entirely a process of biotic interaction. Obviously, there could be a variety of interpretations of the causal processes forming communities. The ecologists conclusions were strongly influenced by the information they obtained from their quadrats and surveys.

The Evidence of Field Studies

In ecological field studies, whether one focuses on plants, animals, or both, the ecologist is faced with interpreting the presence and abundance of hundreds (even thousands) of species consisting of possibly tens of thousands of individuals. Since each species has evolved to fit certain environmental conditions, the of variability in biotic presence and abundance is enormous. Our capacity to understand such patterns depends partly upon our mathematical tools and the availability of instruments to process quantitative data. At the time of Clements, Phillips, and Tansley, these tools were relatively crude. It was possible to see patterns relatively clearly in certain circumstances, especially where the environment was so harsh that it limited the species that could live there. Yet in more temperate or tropical conditions the patterns tended to be confused by gradients of distribution across varying environments.

Environmental conditions varied across space, and individuals of species present in the species pool of the region could disperse, germinate, and grow on those gradients. Individuals would grow and mature in that part of the gradient where the conditions were adequate to meet their requirements, unless other organisms occupied the space. A species would likely be most abundant under the conditions most closely fitting its requirements. Even so, the distributions of species were seldom precise or predictable because both the environmental factors and the biota were discontinuously distributed and were changing dynamically in space and time.

Theoretically, a thorough knowledge of the physiological and behavioral requirements of species would permit us to predict where they would occur. Shelford, author of the influential book *Animal Communities in Temperate America as illustrated in the Chicago Region* used this general approach in his studies of animal communities with considerable success. A consequence of environmental gradients, however, was that communities were seldom, if ever, precisely defined patches made up of constantly occurring species in constant ratios of abundance. Rather, if one was inclined to accept the existence of communities in the first place, each community seemed to be an single example of a type.

A further spatial problem with community analysis, which is the obverse of the problem of deciding who are the residents of a community, was deciding where community boundaries occurred. The distribution of species in continua

across environmental gradients meant that the boundaries of communities were often fuzzy and imprecise. Tansley, in *The British Islands and Their Vegetation,* recognized the problem:

> Much vegetation too, particularly in countries subject to varied human activity, is difficult or impossible to separate into distinct, well-characterized communities—it often presents all grades of mixtures of the elements of several communities in which dominance and layering are confused, obscure, or totally absent. . . . As a general principle, the longer the vegetation is let alone and left to develop naturally, the more it tends to form well-defined communities, and the more these develop relatively constant and well-defined "structures" in relatively stable equilibrium with their conditions of life. (Tansley, 1939, 215)

Pound and Clements in *The Phytogeography of Nebraska* developed a practical approach to the boundary problem, based on their observation of plant distribution in the field. They stated in the section in their book on plant formations:

> Defined accurately, a formation is a piece of the floral covering, the extent of which is determined by a characteristic correlation or association of vegetable organisms, i.e. it is a stretch of land the limits of which are biological, and not physiographical. It can rarely have definite limits, therefore, but must be bounded on every side by a more or less extensive belt in which the features of two adjacent formations are confused. As in the case of species, it often becomes necessary to establish arbitrary limits, within which the preponderance of characteristics must be adopted as the mark of delimitation. (Pound and Clements, 1897, 315)

Pound and Clements were dealing with vegetation in the western United States prairies before that area was greatly altered by agricultural development. They were able to see patterns of gradual change from one community to another.[8] Further, their quadrat data described continuous change in the frequency and abundance of species. Under such circumstances, boundaries are indistinct except where a discrete physical factor is present. In contrast to the unplowed American prairie, the European situation was quite different. There, ecologists were faced with a patchy landscape, long under human control, which was frequently well mapped for military purposes. Owners of land could describe with considerable accuracy the locations of forests, meadows, ponds, and similar communities. Indeed, the ecological historian Oliver Rackham has shown in England that some forest stands persisted from Roman times to the recent period (Rackham, 1980). Under conditions of long-term persistence, the boundary problem may not be difficult to resolve and attention can focus on other matters. Josias Braun-Blanquet (1884–1980), the phytosociologist, for example, recognized that boundaries may be wavy or indistinct (Braun-Blanquet, 1932, 77), but in his method, he placed the quadrats used to describe the stand at the center of a representative section of the community.

In community ecology the ecologist is also dealing with two different kinds of temporal variables. First are environmental features that have temporal dynamics ranging from the day-to-day changes in the moisture conditions of surface soil to geological uplift and erosion that may operate on time frames of thousands or millions of years. Second are the temporal responses of the living organisms that occupy the environment. These responses may range from ancient trees that live hundreds of years to organisms with life cycles that last hours or days. The intersection of these time patterns also results in a great diversity of potential forms and patterns.

As a consequence, the ecologist observes that the communities change over time as well as over space. Where the process is geological in scale, as after glaciation, the communities gradually shift as species invade and disappear, depending upon their capacity to move and interact and on the changing environmental conditions of the site. Where the land has been disturbed by a volcanic irruption, fire, storm, or human disturbance, the site is unoccupied at the start. Organisms occupy the site in waves of invasion and settlement, and as a consequence there appears to be a transition of communities replacing each other.

Development of the Complex Organism Concept

These brief comments on ecological observation of communities suggest that nature may be organized but that close analysis reveals the tremendous complexity of species presence, variability from place to place, and a great deal of change locally in abundance and presence. Where the environment is especially harsh, the patterns may be more orderly, visible, and repeatable. In temperate and tropical environments, however, the environmental conditions are less restricting and biotic interactions make it more difficult to predict and explain community structure.

Several paths through this jungle of complexity, variability, and multiple causation were invented by ecologists. First, a hierarchical approach, copied in part from the taxonomists, was imposed on natural communities. A regional pattern was recognized, representing the most common life form of vegetation within a region—for example, a forest formation under humid climates, or a grassland or desert under a more arid climate. Second, within a region, there is a mosaic of communities of different life forms. In a forested region, besides

forests, one could encounter meadows and bogs, which are caused by local environments under the control of soil, topography, and water level. Finally, if you focus on a single community patch, that patch usually has a particular species composition and abundance that differs from that of the next patch. These local patterns frequently are influenced by the interaction of the biota and the chance occurrence of species.

These patterns create a top-down and bottom-up problem for the interpreter. If one approaches nature from the top, as I have explained in the above paragraph, then one analyzes the pattern by subdividing it and looking for an explanation for each division. The analyst asks, what makes these communities different? How different must the communities be before considering whether there are two or more types of communities in the sample? In the top-down approach the analyst seeks criteria for dividing the whole into its component parts.

Alternatively, if the scientist takes the bottom-up approach, then he or she begins with a collection of individual communities and asks questions about what they have in common. After the criteria for combination are devised, then the ecologist can organize the communities into patterns. The higher units are abstractions that are characterized by the common properties of all the samples but that mimic no individual sample. In this way the ecologist might create an ecological taxonomy, in the same way a taxonomist defines units such as genera, families, and orders that represent hypothesized phylogenetic relationships among the species. Scientists using the top-down and the bottom-up strategies see the world differently and tend to argue strongly about their interpretations.

Ecological science at the time of Phillips's and Tansley's publications was engaged in one these arguments. There were those who saw in the formation, the higher-order abstraction that represented the regional vegetation, as a reality that overlay the finer patterns of the community patches. There were those who focused on the actual stands of vegetation and tried to organize these stands into patterns. This latter group was subdivided into those placing greatest reliance on the presence or absence of species and those focusing on the environmental factors that selected for species. Practically all ecologists of the period were touched by these arguments.

In the United States the interpretation of the vegetation patterns was dominated by the thought of Clements. Clements was raised and educated in the frontier state of Nebraska, and he experienced the great American prairie as a botanical abstraction—the prairie unplowed without bison or native Americans. Clements traveled extensively across the United States as a researcher of the Carnegie Institution, chauffeured by his wife, Edith, who was a trained botanist in her own right. Based on his experience and observations, Clements created a theory of vegetation that was reported in a set of volumes published from 1905 to 1939. The most important of these for this story was *Plant Succession,* published in 1916.

Clements viewed a region as having a characteristic vegetation, called the climax, which was caused by the selection of the regional climate for particular life forms of plants. Of course, Clements observed a variety of communities within a region. He interpreted these different communities through a theory of change or, as he called it, development. The technical term used for this process was *ecological succession*. In Clements's successional theory, all of the stands of vegetation were on trajectories of change converging on the climax type. In some communities change was rapid, but in others change was so slow that the communities might warrant being given a modified climax term, such as a *disclimax* or an *edaphic climax*. Clements invented a complex terminology to fit his theory to what he observed.

Clements went further than a descriptive theory by drawing an analogy between the climax community and an organism. He called the climax a complex organism to distinguish it from the well-recognized individual organism, commonly used in biology. He then asserted that the complex organism went through a life cycle of birth, growth, and development.

Clements had created an awe-inspiring concept of nature. His invention was deterministic, all-inclusive, and internally logical. Even though many did not agree with him, he was an effective advocate for his ideas. Further, as a scientist involved in active field work, he assimilated some critical comments and considerably modified his theory over the years.

In most community studies and especially in the Clementsian theory of succession, the focus was on the biota and the biotic interactions and processes thought to control community dynamics. The environment was considered to be a secondary factor; frequently it was called a stage on which the biota acted a drama. It was implied that living organisms responded to environmental conditions through their physiology and behavior, and in doing so they also influenced and changed the environmental conditions through their "reaction" on and change of physical-chemical factors. Since ecology was a biological subject, it was unlikely that ecologists would be able or interested in examining the environment deeply from a physical-chemical viewpoint. For this reason, there was almost no attempt made to relate the observations of chemists, especially geochemists such as Vladimir Vernadsky and other Russians, to community ecology. Thus, Tansley's emphasis on the interaction of the biota and the environment in the ecosystem was an important conceptual advance and opened the door for the wider use of energy theory and matter cycling in ecology.

Russian physical chemical perspective

ecosystem opened door to introduce "physical" to ecology

SPECULATION ABOUT ECOLOGICAL OBJECTS

It is clear that the interpretation of the patterns of natural communities included an element of abstraction that went beyond the evidence of field observation. The employment of the metaphors of the human community and the complex organism to describe ecological objects and patterns has been typical of the subject. To understand the development of ecological science it is necessary to understand its language and the philosophical concepts that form a deeper context of the subject and its practitioners. For example, Ronald Tobey (1981), in his study of Clements, commented that the use of the organism metaphor for human society by Herbert Spencer and Lester F. Ward in their widely read books probably influenced Clements to use the organism metaphor for his climax community.

Where there were little or no data on mechanisms or experimental experience, ecologists have turned to other sciences and philosophy for allied concepts in interpreting their observations. In assessing the phenomenon it is important to remember that isolated disciplines and specialists were less prevalent in times past. Ecologists shared with other scholars a background in education, which included the study of classical civilizations, languages and literature, and science and mathematics. Thus, as research advanced in new directions, it was easy to dip into a common pool for metaphors that drew connections between what was known and what was new. This approach has tended to be a valuable one for ecological researchers.

John Phillips sought support for the concept of the complex organism from philosophy. He turned to a concept created by Jan Smuts, who had presented his philosophical thought in a 1926 book, *Holism and Evolution,* wherein he called the synthesis of matter, life, and mind—based upon science—*holism*.[9] Smuts noted that philosophers and scientists tended to treat matter, life, and mind as separate phenomena, arguing that they "will appear as a more or less connected progressive series of the same great Process. And this Process will be shown to underlie and explain the characters of all three, and to give to Evolution, both inorganic and organic, a fundamental continuity which it does not seem to possess according to current scientific and philosophical ideas" (Smuts, 1926, 21).

He identified unified structures, which he called wholes, that included physical bodies, chemical compounds, organisms, minds, and personalities. The operative factor which creates wholes is a process of creative synthesis, in which the whole is the synthesis of the parts. For example:

> Taking a plant or animal as a type of a whole, we notice the fundamental holistic characters as a unity of parts which is so close and intense as to be

more than the sum of its parts; which not only gives a particular conformation or structure to the parts but so relates and determines them in their synthesis that their functions are altered; the synthesis affects and determines the parts, so that they function toward the "whole"; and the whole and the parts therefore reciprocally influence and determine each other, and appear more or less to merge their individual characters. (Ibid., 86)

Smuts stressed that the whole is not a simple object, but is complex, consisting of many interacting parts. The parts themselves also may be wholes, as the cells in the body of an organism are wholes. The whole is not a mechanical system, which he characterized as one lacking inward tendencies and where all action is external. All action is through the machine acting on external objects or the action of external objects on the machine. Wholes, in contrast, have inner tendencies that produce more than a machine. Finally, Smuts stressed that wholes are not additional to parts; wholes are the parts in a definite structural arrangement with reciprocal activity and function. To support this idea he used the familiar story of hydrogen and oxygen as chemical compounds with unique properties, which, when combined to form water, have new unique properties as water.

Smuts argued that the concept of the whole transformed the concept of causality: "When an external cause acts on a whole, the resultant effect is not merely traceable to the cause, but has become transformed in the process. The whole seems to absorb and metabolize the external stimulus and to assimilate it into its own activity; and the resultant response is no longer the passive effect of the stimulus or cause, but appears as the activity of the whole" (ibid., 119). Thus, the whole appears as the cause of the external response.

Smuts did not treat the ecological community as a whole, although he did consider human society, families, and nations as wholes. He considered nature to be made up of wholes but was careful to distinguish between nature as an organism, which he denied, and nature as organic through the intensification of the entire field. In Smuts's words, "Nature is holistic without being a real whole" (ibid., 340). He attributed this holistic force of nature not only to humans but to all organisms: "The new science of Ecology is simply a recognition of the fact that all organisms feel the force and moulding effect of their environment as a whole. There is much more in Ecology than merely the striking down of the unfit by way of Natural Selection" (ibid., 340).

The extension of Smuts's holism to the ecological community appears to be Phillips's creation. If Phillips had not used Smuts's thought in the way he did, ecologists probably would have little interest in Jan Christian Smuts or his philosophy.

Conceptual Differences

Phillips's use of Smuts's concept of holism as support for his ecological speculation introduces another problem area that Tansley was addressing with his ecosystem concept. This problem area is complex, and we need to sort out several arguments in order to understand it and use it in this analysis. There are two contrasting arguments that underpin ecological speculation. First is the contrast between materialism and idealism, which was especially active in science and philosophy in the nineteenth century. The materialists argued that all phenomena are material and therefore, potentially at least, able to be understood by applying the methods of science. Ernst Haeckel was a famous representative of this viewpoint. Haeckel was well known as an advocate of Darwin's evolutionary theory and was a vigorous opponent of all spiritual theories and beliefs. The idealist took the opposite view, arguing that there were phenomena that were immaterial and could not be penetrated by science. Religious idealism, of course, posited a God who was above materialism, but scientific idealists also tilted against the materialists. Idealism was an apparently reasonable position to take when little was known about a phenomenon or when a phenomenon was beyond analysis by the scientific methods available at the time.

At the end of the nineteenth century, when Tansley was being educated, there was a well-known debate in biology about an idealistic concept called *vitalism*. The problem involved the nature of life. Although one could analyze a living organism into parts, such as tissues and cells, there was no way to reconstruct the parts into a whole organism and have life. Life seemed to be something immaterial; life was said to represent a vital essence.[10]

Vitalistic concepts were frequently used in biology to explain phenomena that appeared to be unexplainable in materialist terms. One after another, however, these phenomena were explained by conventional research founded on materialist principles, and the vitalist argument was gradually discredited, being held mainly by those defending a religious interpretation of biology. Tansley would very likely have been exposed to these arguments as a student and probably was conditioned to be suspicious of idealist arguments such as holism or the complex organism.

In the ecological story we are considering here the materialist-idealist contrast would be between the description of vegetation on a landscape—such as described by Kerner or Pound and Clements—made up of communities with the observed species compositions, contrasted to Clements's interpretation of vegetation as an organism that grows, matures, and dies. The concepts of the complex organism or the superorganism are idealist concepts that are not researchable using ecological methods of analysis. Certainly, this was one reason for Tansley to argue against the concepts.

reductionism v/s holism

The second argument is between reductionism and holism. Reductionism claims that we can understand the nature of a phenomenon by reducing it to its parts. Analysis of these parts reveals the mechanism of the phenomenon. An engineer will take a reductionist approach when repairing a motor. In mechanical reductionism we are dealing with objects made by humans, for which a plan exists. The problem is to restore the parts to their proper order and link them together to fit the plan. In ecology we are studying phenomena not of our making and for which there is no plan. Research has to develop both the plan and the mechanism.

Holism takes another approach. Smuts's form of holism has been described, but holism can be described in a less idealistic form. Generally, the materialist holist is concerned with how parts are organized to create wholes; that is, the holist is concerned about the rules used to assemble parts into functional wholes. Usually, the scientific holist does not deny the value of reductionism, agreeing that it is necessary to understand the parts and how they act, but adds that it is also essential to understand the rules that are used to assemble the parts to make an object.

The argument between reductionism and holism is an interesting one in ecology because it is unbalanced. First, reductionism seems endless. John Harper introduced his E. P. Odum lecture at the University of Georgia in the mid-1980s by saying that in his research he was digging a hole. Deeper questions arose sequentially as Harper moved from the study of the vegetation of a Welch sheep pasture to the molecular genetics of clover. Because of this endless quest, the reductionist is impatient with the holist—the interesting questions move the reductionist away from synthesis and from the starting point of a particular research. On the one hand, as reductionism proceeds, the reductionist has less and less in common with the ecologist, who is concerned with the broader issues of organization and may even begin to question the value of ecological work in general. On the other hand, the holist understands that the results of reductionist research are always relevant at some level in understanding a phenomenon. Thus, the holist is tolerant of the reductionist agenda and even supportive of it, if the competition is not too keen.

Another problem can emerge in this contrast, which we see in the Phillips's articles. The reductionist continues using conventional methods to go deeper into the analysis. There is no need for the reductionist to use philosophical concepts to explain the findings of research. Philosophy is relevant to the location of the hole, not to the digging of it. In contrast, the holist has made little progress in creating assembly rules. I have already noted the problems of complexity, diversity, change through the environment, and evolution in the natural community—all of which make the ecological system unstable in Tansley's terms. The holist, then, may be tempted to reach for other support for a theory of organization. Usually, the support is a metaphor and the argument is developed analogically. An example of this form of thinking is that if the world is a heat engine, then *x* and *y* follow. If you do not accept the metaphor of the world heat engine, you will not accept the logic that follows. Analogical thinking is valuable to establish new hypotheses to follow in research in an area where little is known. It is less valuable where the research plan is clear.

The complexity of the problem in the philosophy of science suffices to show the underlying problem in the Phillips's articles. Both Phillips and Tansley were materialists. Phillips was a holistic materialist, using Smuts philosophy of holism to support the concept of the complex organism. Tansley, aware of the split between reductionist and holistic materialism, which divided ecology into two unreconcilable parts, sought a common ground. His ecosystem concept was offered as a bridge. In developing the ecosystem concept he avoided biological and organismic theories altogether. They were a trap that led to emotional debates between biologists and ecologists. Rather, he presented a physical theory that was founded on the concept of equilibrium. Although Tansley does not say so directly, equilibrium and stability provide the foundation for assembly rules. The more stable the system, the more likely it is to persist; systems tend to move toward equilibrium, and so on.

Whitehead's Science and the Modern World

In coming to this position Tansley is not unique, although his term, *ecosystem*, is unique. Many other scientists and philosophers were trying to find links and bridges that would prevent intellectual life from shattering into parts that could not communicate with each other. One thinker that was very close to Tansley in his ideas and who was referred to by Tansley and rejected as an "organicist" was Alfred North Whitehead (1861–1947). Eugene Hargrove pointed out in his book *Foundations of Environmental Ethics* that Whitehead's holistic concepts also were very near those of Aldo Leopold (1887–1948), the famed wildlife biologist and conservationist from Wisconsin who at that time was developing a powerful statement of practical ethics. In Leopold's *Sand County Almanac*, he stressed that "a thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise" (Leopold, 1949, 224–25).

Whitehead much more than Smuts provided a philosophical ground for the holistic ecological concepts Leopold and others advanced. In 1925, Whitehead presented the Lowell Lectures at Harvard, which were published together with some additional essays as *Science and the Modern World*. In this book

> We think Dr. Clements easily establishes his case for a "system" and his views of "The Essentials of a System," based on the absolutely fundamental importance of the habitat, its effect on the plant and the reaction of a plant upon it, may be said to be almost self evident. . . . The ecological investigator in the midst of vegetation finds himself in the presence of a state of equilibrium between the organized and the unorganized, between "The Habitat" of the one part and "The Formation" of the other part. (Blackman and Tansley, 1904, 203, 232)

In 1911, in *Types of British Vegetation,* Tansley commented;

> It may be said that we ought not to occupy ourselves with synecology till we have a complete or an approximately complete knowledge of autecology, but this is a mistaken notion. It might as reasonably be contended that we ought not to study the phenomena presented by the nations and races of men before we know all about the physiology and psychology of the individual man. As a matter of fact the study of synecology is considerably in advance of autecology (which is indeed still in a very backward state of development) and the progress made has amply justified the attention devoted to the wider though less fundamental branch of the subject. (Tansley, 1911)

In 1926, in *Aims and Methods in the Study of Vegetation,* Tansley and T. F. Chipp (p. 141) made the point:

> How are we to draw the line between those which act as *members* of the community and those which are to be considered external—whether "hostile" or "friendly"—to it? Some ecologists have tried to get over the difficulty by considering *all* the organisms, animals and plants together, living in one place and mutually acting upon one another, as members of the community, as a biotic unit. There is a good deal to be said for this conception from a philosophical point of view, for it is really the whole of the living organisms together, *plus* the inorganic factors working upon them, which make up, in a climax community, a "system" in more or less a stable equilibrium. But such a "system" considered fundamentally, that is, physically, must include the "inorganic" factors of the habitat and these obviously cannot be considered as "members" of the community, and if we take the inorganic factors as external, why not biotic factors such as grazing animals?

The concept of a system is ancient and had wide use in science. In conventional terminology system meant a complex in which the parts interacted to

produce the behavior of the whole. In the period between the two world wars, however, system science emerged as a separate subject. Ludwig von Bertalanffy (1901–72), a major figure in German theoretical biology (Davidson, 1983), describes this period of development of the system concept (Bertalanffy, 1952): "The future historian of our time will note as a remarkable phenomenon that, since the time of the first World War, similar conceptions about nature, life and society arose independently, not only in different sciences, but also in different countries. Everywhere we find the same leading motifs; the concepts of organization showing new characteristics and laws at each level, those of the dynamic nature of, and the antitheses within reality. (Bertalanffy, 1952)

Bertalanffy traces the development of a philosophy of systems dynamics from Heraclitus, the sixth-century B.C. Greek philosopher noted for his ideas on universal flux, paradox, and the unity of all things;[11] Cardinal Nicholas of Cusa in the Italian-German renaissance, who taught the infinity of the universe and the coincidence of opposites; and Goethe, the father of morphology, to the philosopher Nicolai Hartman, who in 1921 described a system whereby forces balance one another and lead to a stable configuration, which is organized in a hierarchical pattern. Bertalanffy's list of founders could be expanded to include other philosophers and scientists, depending upon the aspect of systems theory one wished to emphasize. For example, the American ecologist Charles Christopher Adams expressed almost identical thoughts to those of Bertalanffy but derived from Herbert Spencer in 1915 and 1918 publications.

Systems science was a technical application of holistic, materialistic philosophy. Paraphrasing the systems scientist Mario Bunge (1979), the typical scientist or engineer applies a particular science to the general problem, but the systems expert deemphasizes the physics, chemistry, biology, or sociology of his or her system, focusing instead on its structure and behavior and the possibility of duplicating this behavior with that of a system of a different kind. It was possible to develop conceptual models of system behavior in the between-the-world-wars period, but operative, manipulable models required mechanical computers, which were years in the future. Thus, systems science in this period had a focus—the discovery of the assembly rules through which the parts of systems could be organized into wholes—and an objective—to connect isolated systems into networks, but lacked a method.

Sir Arthur George Tansley proposed the concept of the ecosystem as a solution to several vexing conceptual problems in ecology, introducing the term in his contribution to a festschrift for Henry J. Cowles. Tansley was disturbed by a set of articles by the South African plant ecologist John Phillips that illustrated in Tansley's mind several of the problems he wished to counteract.

Whitehead examined the history of Western thought, especially the interaction of science and philosophy. He contrasted the pattern of medieval thought, which assumed a world of order created by God and understandable to the rational mind, with the modern concept of a particulate, materialistic world in which order, if it exists, is relative and momentary. In these systems every detail and event was supervised and ordered, and the search into nature vindicated a faith in rational organization. Further, every occurrence could be correlated with its antecedents in a definite manner, exemplifying general principles. The medieval world's interest in nature began in the arts, for example, in the curling tendrils of vegetation on cathedral columns, and possibly more powerfully through the monastic experiments in agriculture and forestry, which were among the first steps toward a modern scientific view. In the Renaissance the focus shifted to the immediate, simple fact of observation and experience and the belief that individual humans and higher animals were self-determining organisms. This shift created a profound revolution in thought and made modern science possible.

Like Tansley, Whitehead recognized the contradiction in science, which stressed the primacy of fact and individual interpretation of fact, yet had the grander purpose of discovering patterns or order in the natural world. According to Whitehead, this contrast between a deterministic and relativistic interpretation of particular events, as well as generalizations leading to broad conclusions based on rational thought, was a general problem for science and culture. While the contradiction might be avoided within the physical and chemical sciences because the wholes recognized by these scientists remained physical, the problem was central to the biological and social sciences. In ecology the contrast was illustrated by the determinist theory of Clementsian succession, cited by Phillips, as contrasted to the relativistic approach advocated by Henry Gleason (1882–1975) of the University of Illinois. Gleason (1926a, 1926b, 1939) stressed the role of individual plants to invade and grow on the environmental gradients and declared the plant association was a "mere coincidence."

Whitehead pointed out that these points of view resulted in three positions: dualism, in which both individualism and holism coexist, or monism, which in turn places individualism within holism, or holism within individualism. Whitehead accepted none of these. Rather, he proposed a bridge position designed to solve the contradiction: "The doctrine which I am maintaining is that the whole concept of materialism only applies to very abstract entities, the products of logical discernment. The concrete enduring entities are organisms, so that the plan of the *whole* influences the very characters of the various subordinate organisms which enter into it. In the case of an animal, the mental states enter into the plan of the total organism and thus modify the plans of the successive subordinate organisms until the ultimate smallest organisms, such as electrons, are reached" (Whitehead, 1944, 115). For Whitehead, biology was the study of larger organisms, and physics was the study of smaller organisms. The character of these organisms, Whitehead postulated, was the "event," the ultimate unit of natural occurrence. Tansley had used a similar metaphor in formulating the ecosystem concept, derived apparently from a popular book on science, *The Universe of Science,* by H. Levy. Two patterns characterize an event: "Namely, the pattern of aspects of other events which it grasps into its own unity, and the pattern of its aspects which other events severally grasp into their unities" (ibid., 174).

The event had a temporal aspect, an endurance, a retention of form or value over time. It repeated the shape exhibited by the flux of its parts, so the entity had a life history represented by the dynamics of its parts. Additionally, the life history of the individual entity was part of a larger, deeper, more complete pattern and may be dominated by aspects of this larger pattern. Whitehead called this the *theory of organic mechanism.* Thus, he concluded that there were two aspects involved in the development of nature:

> On one side, there is a given environment with organisms adapting themselves to it. . . . From this point of view, there is a given amount of material, and only a limited number of organisms can take advantage of it. The givenness of the environment dominates everything. . . . The other side of the evolutionary machinery, the neglected side, is expressed by the word *creativeness.* The organisms can create their own environment. For this purpose the single organism is almost helpless. The adequate forces require societies of cooperating organisms. (Ibid., 163)

In these writing Whitehead used the theory of biological evolution to provide a motive force to create dynamic interaction. Tansley used the physical concept of equilibrium to serve this purpose.

The System Concept

It remains to explore Tansley's use of the concept of system in his use of the term *ecosystem.* Tansley used the systems idea frequently in his writing. It served to organize his concern about the organization of nature. For example, as F. F. Blackman's and Tansley's review of Clements's *Research Methods in Ecology* explained:

> The book is divided into four parts or "chapters." The first, under the heading "The Foundations of Ecology," discusses "The Need of a System," and contains the ideas upon which we have already commented.

Tansley's ecosystem concept was a physical concept that stressed that both the physical-chemical environment and biotic organisms acted together to form an ecosystem, which was in turn formed part of a hierarchy of physical systems from the universe to the atom. The physical concept of equilibrium guided the organization and maintenance of ecosystems. The stability or persistence of the system involved its movement toward equilibrium. Tansley was quite modern in entertaining the possibility that ecosystems seldom, if ever, achieved stability.

The ecosystem concept emerged in a theoretical argument. It was not the result of a technical study and was not presented as the synthesis of field observations. Further, Tansley never used the ecosystem concept in his studies, although he did use the concept in later conceptual writings. Rather, the term emerged at a time receptive to such concepts. Systems science had begun its development, and while Tansley distanced himself from Alfred Lotka, the American physical biologist, and Bertalanffy's efforts to create a biological systems theory, his ecosystem concept fit the emerging pattern of systems science. Philosophers such as Whitehead were also formulating theory in terms similar to Tansley's ecosystem, but again Tansley did not avail of them to support his concept. Rather, he depended upon the connection of the ecosystem to the physical sciences, the most precise and mathematical sciences, and the concept of physical equilibrium to convince his audience.

Tansley did not clarify whether he considered an ecosystem to be an object of nature or something else. His event-focused physical orientation may have favored treating the ecosystem as an event in a physical field of dynamic process. Yet Tansley did not use the physical field concept in his presentation, nor did he refer to the flow of energy or matter cycles, both topics that would later become central elements of ecosystem studies. Because he was unclear on these points, ecologists tended to misuse the term *ecosystem* as a more modern expression for the community concept or Clementsian complex organism and thus maintained the confusion that Tansley was trying to overcome.

Tansley's strategy can be understood as a consequence of his frustrating experience to obtain recognition both for ecology as a serious science in Britain and for himself within British academic life as an ecologist with high standards for technical work and writing. He grew up in a time when the great discoveries in physics at the Cavendish Laboratory at Cambridge—close to the Botany School where Tansley taught—excited scientists everywhere. Thus, Tansley chose a familiar and acceptable authority on which to anchor his ecosystem concept.

CHAPTER 3

The Lake as a Microcosm

I have suggested that Arthur Tansley formulated the ecosystem concept solution to a conceptual argument that divided plant community ecology i two opposing camps. One group emphasized the significance of the indivi stand of vegetation and organized these stands into hierarchies of commu organization. The other hypothesized that vegetation was a complex organ that developed, matured, and became senescent. Tansley was aware how s arguments could act against the reputation of a field of inquiry and was acu conscious of the low esteem in which his fellow physiologists, morpholog and geneticists held ecology. Part of Tansley's motivation in creating the system concept was a desire to find a bridge that would link these two poin view into one ecological approach.

I have also suggested that the language Tansley used for his concep ecosystem was derived from the scientific and philosophical ideas cur during the early twentieth century in England and the United States. Am these ideas was the concept of a system, as used widely in science and tech ogy, and that of a physical equilibrium. Unlike the ecologist's communit complex organism, Tansley's ecosystem was composed of both the phys chemical environment and the entire biota, not just the plants or animals. T concepts are related and together they represent a different aspect of broader ideas that were derived from both the scientific interpretation of na and holistic concepts of Western European philosophy. Although Tan attached his ecosystem concept to the physical sciences, he carefully avoi

Chapter 2: Genesis of a Concept

1 The Tansley biographical material includes Sir Harry Godwin's three publications, two of which concern Tansley directly (Godwin, 1957, 1977) and the other (Godwin, 1985) with Cambridge, England, and includes a discussion of Tansley in this context. G. Clifford Evans, in his 1975 presidential address to the British Ecological Society, explored the development of Tansley's ideas, including the ecosystem concept. In addition, Tansley presented several analyses of the ecological sciences of his own, including a review of British ecology over the past quarter-century (1939b), the value of science to humanity (1942), the early history of modern plant ecology in Britain (1947), and *Mind and Life* (1952).

Few of Tansley's papers remain, although Sir Harry Godwin, responding to a letter from R. E. W. Maddison, The Royal Society, about Tansley's papers, said that he saw no files of correspondence, notebooks, or manuscripts when he went through Tansley's office after his death, and as a consequence, that he thought these materials were small in volume or had been disposed of by the family. The primary collection is in the Botany School, Cambridge, along with Tansley's reprint collection. In addition, there are several important letters of Tansley in the Frederic Clements Collection, American Heritage Center, University of Wyoming, Laramie (hereafter referred to as the Clements Collection). Tansley's library was inherited by Godwin but was disposed of upon Godwin's death. Peter Grubb, Cambridge, owns a small set of Tansley's ecological volumes.

2 A letter, dated 18 Dec. 1918, from Tansley to Frederic Clements referring to a quotation in German from Professor Gams, Innsbruck, about Clements, said that Gams was "very angry indeed! Almost as angry as Professor Bower of Glasgow on the subject of my 'Bolshevism.' I've been getting some experience in the 'Gentle art of making enemies' lately. The more you keep your temper the madder they get. Reactionary forces are pretty strong here, and it will be a hard struggle to get anything progressive done. But I am going to have a good try. In regard to the 'reconstruction' discussion the enemy has had his innings and the end of it will be mainly on my side. But it is a long step forward to deeds, especially when the high places are occupied by the enemy. Fortunately my livelihood does not depend upon the favor of the exalted reactionaries. But I often look with envy on your 'hope-filled western skies' (Chicago *Alma Mater* hymn).

Nevertheless, my job is on this side. I am sure though it is sometimes depressing to realize that now the Boche is beaten we have to begin another fight in the spiritual sphere." Letter, Clements Collection.

Clements's response to Tansley, 14 Feb. 1919, was: "I was greatly interested in Bower's article about the newer teaching. Naturally you are in a difficult position with the most important chairs occupied by men of that type. It is marvelous how thoroughly hide-bound static subjects such as morphology can make a man. Or perhaps it is merely that everything tends toward stabilization and nothing but the extremist devotion to progress can prevent it either in the individual or his work." Letter, Tansley Papers, Botany School, Cambridge.

Finally, in a letter to Clements, 12 July 1923, Tansley described his relief to be free of the Cambridge conflict. "I am most thankful to be free of obligations as University Lecturer—I scarcely realized until I had actually resigned what a strain being part of an uncongenial, uncorrelated organism like the Botany School, Cambridge, really was." Letter, Clements Collection.

3 On 12 Jan. 1923 Clements wrote Tansley asking about his decision to resign from botany: "I have been hoping to hear from you with reference to your decision and plans for some number of the Journal of Ecology, I can understand why you have no time to spare for letters. However, I am anxious to know what you are planning to do, and still hope that you have been able to arrange matters so that you will not have to forsake ecology altogether. Perhaps it is selfish on my part because I am not at all sure that your new field may not have greater opportunities for distinct and distinguished services." Letter, Tansley Papers, Botany School, Cambridge.

On 8 March 1923 Tansley answered, "Probably I shall cease to be a professional botanist after the term, though for the present, at least, I shall continue to edit the two journals. . . . Admonson is going to the Cape and will be a terrible loss to me—I need a good 'florist' at my elbow. Together with the 'conservatives in authority' his departure will help make me spend more time at psychology and less at ecology. The last year or two I have been pursuing both, and though my power of work is much better than it was, largely I think to the release of powers through emotional clarification—the double pull is a considerable strain." Letter, Clements Collection

Then, on 30 May 1923, in another letter to Clements, Tansley wrote, "You will be interested to hear that I have now definitely resigned my University Lectureship in Botany. I am tired of official lecturing and I do not see the possibility of doing anything better in the teaching line within the existing framework, which I can not alter. I go to Freud again in October for some months, but for the present, at least, I shall continue to edit the two journals. It is likely that I shall take my whole family with me to Vienna." Letter, Clements Collection.

4 Tansley, 1935, 284. In the second decade of the twentieth century, Frederic Clements published his monumental book on plant succession and became the individual most closely associated with the topic. By the time of the Cowles festschrift, Tansley had distanced himself from Clements extreme interpretations. Their difference of opinion, however, had been apparent as early as 1915 and 1916 (see letters, Clements Collection). Clements expressed the hope that they could come to an agreement over the meaning of the concept of habitat and formation. In Tansley's own discussion of succession (1929), he analyzed the concept in a broad and advanced way, anticipating many of the views of later antagonists of the Clementsian concept. For example, Tansley states that "a climax community is a particular aggregation which lasts, in its main features, and is not replaced by another, for a certain length of time; it is indispensable as a conception, but viewed from another standpoint it is a mere aggregation of plants on some of whose qualities as an aggregation we find it useful to insist. . . . These selective syntheses are essential to the progress of science, and the particular ones

mentioned are of very great value, as I have tried to show, in the study of vegetation and ecology. But we must never deceive ourselves into believing that they are anything but abstractions which we make for our own use, partial syntheses of partial validity, never covering *all* the phenomena, but always capable of improvement and modification, preeminently useful because they direct our attention to the means of discovering connections we should otherwise have missed, and thus enable us to penetrate more deeply into the web of natural causation." "It is the special credit of American ecology, and in the first place of the labors of Cowles and Clements, followed by a host of gifted workers, that laid stress upon the successional way of viewing vegetation at a critical epoch in the development of the science" (p. 686).

Tansley's view of succession was more balanced and more empirical than Clements's. In this sense he is closer to Cowles—who described the vegetation of the Lake Michigan dunes and interpreted it within conventional plant ecology—than to Clements, who created a new ecological paradigm based on his observations of vegetation change.

5 Tansley asked Clements about Phillips in two different letters. On 17 July 1924, he asked "Who Is Phillips?" and on 12 October 1924, "I am curious that I haven't heard of Phillips. One would have expected he would have contributed to the perambulations and discussions we had on Empire vegetation work at the last Imperial Botanical conference in July. I wonder if the secretary missed him, so that he never heard of it?" (Clements Collection).

Phillips, in a tribute to Clements published in *Ecology* in 1954, described his own academic history. Phillips was educated at Edinburgh but moved to South Africa in 1922. He remained in Africa throughout his career and was a professor of botany at the University of Witwatersrand from 1931 to 1948.

6 Phillips, 1931, 20. The references to Clements are 1905, 1916, and Clements, Weaver, and Hanson, 1922; to Tansley, 1920 and 1929; to Smuts, 1926.

7 Tansley, 1935, 285. Phillips, however, wrote about thirty years after this article (in 1954): "Tansley, in this journal in 1935 (16:284–307), in a kindly manner, hinted that my papers in the Journal of Ecology (1934–35:22, 23) on succession, development, the climax and the complex organism suggested a tendency to absorb the pure milk of the Clementsian word. I still hope to publish a corrective to my old friends' courteously incorrect assessment." Even so, Phillips's last comment on Clements was adulatory and did not deal directly with Clements's basic concepts.

8 In a letter, Clements to Tansley, 6 Dec. 1916, Clements writes, "I fully appreciate the great advantage we have over here with our enormous stretches of fairly uniform untouched climaxes" (Tansley Papers, Botany School, Cambridge University).

9 The term *holism* was derived by Smuts from the Greek *holos,* or "whole", and the English suffix *-ism.* There is a deeper origin for this English word, however. Barnhardt (1988, 1229, 1234) states that the original spelling of whole was *hol,* which was derived from Old English *hal.* The *wh-* spelling for words beginning in *ho-* began to appear in the 1400s. Thus, Smuts was doubly correct is choosing his spelling over the widely used *wholism.*

10 An élan vital, Henri Bergson (1911).

11 Wheelwright (1959) interprets the relevant fragments of Heraclitus's writings that have survived as follows: "Everything flows and nothing abides; everything gives way and nothing stays fixed. You cannot step twice into the same river; for other waters are continually flowing on" (p. 29). Opposition brings concord. "Out of discord comes the fairest harmony" (p. 90). "And, it is wise to acknowledge that all things are one" (p. 102).

Chapter 3: The Lake as a Microcosm

1 The term *limnology* was coined by Forel from the Greek *limne* or lake (Rodhe, 1974, 67). Einar Naumann and August Thienemann (1922), however, in proposing the formation of an international association of theoretical and applied limnology wrote: "Limnology is the science of fresh water as a whole, and includes everything that affects fresh water. It falls therefore into two parts, hydrography and biology." Hydrography includes the study of the form of the lake basin, deposition processes, physics of water, temperature patterns, water chemistry, and so on.

2 I am indebted to Sharon Kingsland (1985) for her information on Forbes and for pointing out his use of the ideas of Spencer and Darwin. Spencer is one source of the concept that communities are organisms. He stated that societies of humans are organisms and drew analogies between the development of the individual and development of society. Indeed, he used the phrase "structure, function, and development of the system" in referring to social systems (Andreski, 1971) . The language of Spencer is almost exactly that used by ecologists in discussing ecosystems.

3 Ward and Whipple (1918) used the term *society* to refer to the organisms living in specific habitats. For example, there were limnetic societies and littoral societies. Limnetic societies were divided into "placton" (sic) and "necton" (sic). There were also lentic societies in stillwater and lotic societies in flowing water.

4 In Forbes's (1907) words: "By 1879 . . . a virtually new situation had arisen in science, and especially in scientific education. Under the influence of Darwin and Agassiz and Huxley, a transforming wave of progress was sweeping through college and school, a wave whose strong upward surge was a joy to those fortunate enough to ride on its crest, but which smothered miserably many an unfortunate whose feet were mired in marsh mud. This wave reached central Illinois in the early seventies" (p. 895).

5 Thienemann, 1925, 20–22. Trans. F. B. Golley.

6 Harald Sioli, an emeritus director of the Max Planck Institute for Limnology at Plon, Germany, stated (in a letter to the author, 12 Feb. 1988): "Thienemann, in