A History of the Ecosystem Concept in Ecology

More than the Sum of the Parts

A HISTORY OF THE ECOSYSTEM CONCEPT IN ECOLOGY

MORE THAN THE SUM OF THE PARTS

FRANK BENJAMIN GOLLEY

The ecosystem concept—the idea that flora and fauna interact with the environment to form an ecological complex—has long been central to the public perception of ecology and to increasing awareness of environmental degradation. In this book an eminent ecologist explains the ecosystem concept, tracing its evolution, describing how numerous American and European researchers contributed to its evolution, and discussing the explosive growth of ecosystem studies.

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—*Ecology*

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CONTENTS

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

PREFACE

I was motivated to write this book for a variety of reasons. First, I intended to write a critical review of the ecosystem concept. All phases of science need critical review and ecology is no exception. Review is a bit like checking one's bearings when on a hike in the mountains. It is important to know where you are. The ecosystem has been a key concept in the development of modern ecology, yet today it is widely misunderstood and misused. Many of my students in the 1980s came to graduate school thinking the ecosystem concept was old-fashioned and that it had been rejected by ecologists. It was clear that ecologists did not share a common understanding of the concept, nor were they agreed on how ecology should be taught to the beginning student. Part of the reason for this situation is the information explosion in ecology. As I collected data for the review of the ecosystem concept, I became overwhelmed by the quantity of information. In seeking to organize it, gradually I became convinced that a chronological organization would be more useful than the traditional division into structure and function.

Therefore, the project evolved from a scientific review into a history of the ecosystem concept. Ecology as a subject is little more than one hundred years old, and recently it has experienced a period of rapid growth in public awareness. I have found few students, and few people, who have a clear understanding of the development of scientific ecology. In fact, the time frame for analysis of a topic or a concept in a graduate ecology course seems to have a depth of only five to ten years. Although this limited perspective reflects the amount of

information students can assimilate in any subdiscipline of ecology, it also reflects the fact that there are few historical studies of ecology: it is taught as if it had no history. Thus the historical approach is distinctly useful beyond the focus on an important concept.

It is obvious that the review of a scientific concept and its history represent two very different perspectives. The study of history is a discipline that has its own methods, canons of scholarship, and standards. Contrary to what many scientists might imagine, a history is not merely a chronological listing of past events. Rather, the events must be examined, questioned, and placed in an appropriate context. Studying the history of ecology is like peeling an onion. Once one layer is removed, a new layer appears, so causation and motivation are linked, layer upon layer, in time. Further, the interaction of the historian with these interpretations changes as the story becomes more and more complex. There is no general history of ecology, no set of facts that represents ecological change in time. Instead, each event is as unique as each individual organism is to the field ecologist; each historical interpretation is as limited as each ecological hypothesis; and each historian is as limited by his or her experience and capacity to understand as each ecologist is in beginning a new research project in a new habitat.

I can cite an example of this phenomenon, associated with this particular story. In September 1992, Joel Hagen published his history of the ecosystem concept in *An Entangled Bank*. Hagen and I use approximately the same material, but we each tell two very different stories about ecosystem ecology. His approach is to embed the ecosystem concept in a history of American and English ecology. My approach has been to focus on the concept and the individuals contributing to concept development and then to consider causal factors that led to the pattern we observe. Joel Hagen is a historian and comes to the story from outside, as it were; I was a participant in the story and approach it from within. The result is two different books.

All disciplines have standards by which the usefulness of their creations are judged. I would apply two criteria. The first is generality. Does the study open the window to larger vistas? Does it provide links to other events occurring at the same time? Does it link our present concerns with those of ecologists in other times and places? The second is uniqueness. Does it possess a singular voice so that the individual behind the interpretation becomes visible? The voice of Fernand Braudel, the late master of French history, is distinct and clear even in translation. I can make the same comment about contemporary environmental historians such as Bill Cronin, Al Crosby, and Donald Worster. I hope that in this book I have satisfied these criteria.

As I proceeded in writing this book, I realized more and more that my own

role in the development of the ecosystem concept and in the many activities that created the concept as we know and use it today influenced my perspectives and interpretations. My view has been that of a participant, not merely of an observer. I have tried to check the tendency to rely on memory and express personal convictions, yet inevitably at times the personal voice intrudes. For this reason, I provide more biographical comment than is usual in a preface.

My particular approach to this enterprise comes partly from my family background and partly from my graduate training. My maternal grandfather, Lewis C. Baird, was a historian, army officer, and engineer. He wrote several personal histories, as well as the *History of Clark County Indiana,* published in 1909, which was one of many county histories of that era. I was raised with my grandfather's histories as models of family and public life. As a graduate student at Washington State University when I began a master's program in zoology and wildlife management, Herbert Eastlick was chair of the department of zoology and Helmut Buechner was my major professor. These men taught that a scholar should know his or her subject critically and that the library was as important to the ecologist as the laboratory or field. I was required to make a bibliography of the literature pertaining to my research topic, to read all of the papers and books in this literature, and to incorporate them into my thesis. Each evening I carried a shoe box that contained my bibliography on three-by-five cards to the library. Thus I became attracted to the bibliographic review and thorough analysis of a topic from the beginning of my scientific career.

My graduate training continued at Michigan State University, where I was fortunate to be guided into a study of the energetics of a food chain by Don W. Hayne. This study was one of the first of its kind, and through it I met Eugene P. Odum and became associated with him at the University of Georgia, where I have remained throughout my career, working on ecosystem studies, among other projects, and have been involved in many of the major ecosystem efforts nationally and internationally. These efforts included the International Biological Program, the ecosystem studies of the U.S. Atomic Energy Commission, the UNESCO Man and Biosphere projects, and most recently work with the organization of the Association of Ecosystem Research Centers. I served as division director of the National Science Foundation Division of Environmental Biology (1979–81), which provides financial support to ecosystem studies.

One can, of course, justify an interest in reviewing a concept on other than personal grounds. In 1964, the biologist Bentley Glass wrote in defense of reviewing in the *Quarterly Review of Biology*. Glass quoted Robert Graves: "The scholar is a quarryman, not a builder, and all that is required of him is that he should quarry cleanly. He is the poet's insurance against factual error." Glass goes on to argue with Graves:

> But I would say that the real scientist, if not the scholar in general, is no quarryman, but is precisely and exactly a builder—a builder of facts and observations into conceptual schemes and intellectual models that attempt to represent the realities of nature.
>
> This insight, this vision of the whole of nature—or at least some larger part of it—exists in all degrees among the individuals we call scientists. The man who adds his bits of fact to the total of knowledge has a useful and necessary function. But who would deny that a role by far the greater is played by the original thinker and critic who discerns the broader outlines of the plan, who synthesizes from existing knowledge through detection of the false and illumination of the true relationships of things a theory, a conceptual model, or a hypothesis capable of test?
>
> The creativity of scientific writing lies precisely here. The task of the writer of a critical review and synthesis that fulfills these objectives and meets these criteria is not only indispensable to scientific advance, it surely constitutes the essence of the scientific endeavor to be no mere quarryman but in some measure a creator of truth and understanding. The aesthetic element that makes scientist akin to poet and artist is expressed primarily in this broader activity.

In this examination of the development of ecosystem studies, I also have been guided by a model from Arthur Lovejoy, who wrote *The Great Chain of Being*. Lovejoy subtitled this book "The History of an Idea," and his phraseology captured my imagination. The ecosystem is an idea, a powerful idea, and a popular idea. I have tried to keep this always in mind. Later, I learned that the study of the history of ideas is a subdiscipline of history. I do not pretend to have gone that far. Rather, I use the phrase metaphorically to describe my intent and goal.

Finally, I apologize for not being encyclopedic. There is an advantage to such an aim, and my first intention was to include everything pertinent to the story within this volume. But scientific literature is not a linear stream of papers and books, each building on the other. Rather, it is a complex of forward motions, turnings, repeating, and contradictions. Individuals enter for a time, are active, and then turn to other pursuits. Therefore, instead of an encyclopedia, I have adopted the metaphor of the drama, with a stage, principal characters, and a cast of hundreds. Unfortunately, because of space and time restrictions, I have had to exclude many of those standing immediately offstage. The script moves through time in a straightforward fashion, but each act has a separate identity.

What do we now have? We have elements of a review, a history, a drama, and certainly, a story. Bill Cronin, at a Duke University gathering of environmental historians, said that history is storytelling. He emphasized that since we have a story, we should be aware of a teller of the tale, a store of past events from which the teller selects, an audience, and an environment that encloses the storyteller and his audience. I hope that each of these specific elements is clear in what lies ahead.

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CHAPTER 3

The Lake as a Microcosm

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

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

going very far beyond scientific experience with his concept. Even so, he opened a door for those with a desire to find universals in nature to create a new ecological synthesis. As far as we can tell from the literature, he never employed the ecosystem concept in his own scientific work.

The tradition in which Tansley worked was terrestrial plant ecology. He initiated plant surveys of the British isles and wrote extensively on British vegetation. The ecosystem concept was presented as a solution to an argument about vegetation terms and concepts. Yet there were other ecological traditions that addressed these questions from other perspectives. One of the most important was fresh water ecology, or as François Alphonse Forel (1841–1912) named it in 1892, *limnology*.[1] Tansley was undoubtedly aware of the advances made in limnology since botanically oriented treatises on freshwater ecology were published frequently in the two technical journals he edited, *The New Phytologist* and the *Journal of Ecology*. Still, Tansley did not cite articles from this tradition in support of his ecosystem concept. Indeed, the aquatic ecologists were well ahead of terrestrial ecologists in developing an operative system concept.

One of the first of these aquatic system concepts was the idea of a lake as a microcosm, expressed by Stephen Alfred Forbes (1844–1930), a distinguished Midwest American biologist. Forbes founded the Illinois State Laboratory of Natural History (later the Illinois State Natural History Survey) in 1878, was appointed state entomologist in 1882 and head of the department of zoology and entomology at the University of Illinois in 1884. He was strongly influenced by Herbert Spencer,[2] especially in his employment of the concept of the balance of a system. Forbes described a lake as "an old and relatively primitive system, isolated from its surroundings. Within it matter circulates, and controls operate to produce an equilibrium comparable with that in a similar area of land. In this microcosm nothing can be fully understood until its relationship to the whole is clearly seen. . . . The lake appears as an organic system, a balance between building up and breaking down in which the struggle for existence and natural selection have produced an equilibrium, a 'community of interest,' between predator and prey." In this 1887 statement, made almost fifty years before Tansley formulated his concept of the ecosystem, Forbes anticipated several of the points Tansley was trying to make, and in one sense at least, went beyond Tansley. Forbes's vision of a lake as a isolated object, a system in which cycles of matter maintain an equilibrium between the forces of production and decomposition, has—more than one hundred years later—a contemporary cast.

The ideas of Forbes were not well known outside of the Midwest. Part of the reason for his obscurity was that he published in the *Peoria* (Illinois) *Science*

Association Bulletin (later republished in the 1920 *Bulletin of the Illinois Natural History Survey*). August Thienemann, who would likely have made use of Forbes's ideas, did not refer to him in his 1925 survey of European freshwaters, *Die Binnengewasser Mitteleuropas*. Another reason for the delay in implementing Forbes's microcosm concept was that the development of a functional approach required a strong descriptive base. It is necessary to know what organisms live within the system and to understand their linkages with the environment before they can be organized into a system. It was not until the period between the first and second world wars that enough information had been accumulated to take this step.

Forbes's 1887 image of the lake as a microcosm introduced another group of scientists who made a much greater contribution to the development of the ecosystem concept than did the terrestrial vegetation scientists. Limnologists were distributed across the northern latitudes coincident with the distribution of lakes on the landscape. The postglacial and mountain landscapes in North America, Europe, and Asia provided numerous opportunities for the formation of lakes, and as J. G. Needham and J. T. Lloyd showed in their 1916 textbook for North America, biological field stations developed on the shores of these habitats early in the twentieth century.

The scientific study of lakes began with Forel's three-volume study of Lake Geneva during the last decades of the nineteenth century. Work in limnology in general, and in lakes in particular, proceeded rapidly, so that by the early twentieth century there was a large amount of literature on the subject. In 1916 James G. Needham and J. T. Lloyd of Cornell University published an elementary textbook on fresh water biology, and in 1918 Henry B. Ward of the University of Illinois, and George C. Whipple of Harvard University, collaborated to produce their famous *Fresh Water Biology*. Both of these volumes were devoted mainly to the biology of individual taxa, although Needham and Lloyd discussed aquatic "societies" in their volume.[3]

The development of limnology advanced rapidly in the midwestern United States and northern Germany. In the United States the science was stimulated by the presence of lakes and the establishment of new universities. The University of Wisconsin was constructed on the shore of Lake Mendota and Cornell University was located on the Finger Lakes of New York. The University of Michigan was surrounded by many small glacial lakes. All of the new institutions became centers of limnological studies. The settlement of the midwestern states had occurred only a few years before, and the formation of universities provided opportunities for the organization of new subjects and approaches to education and research. For example, when Edward Asahel Birge (1851–1950), who organized the work in Wisconsin, began his professorship at the

University of Wisconsin in 1879, his was a one-man department of biology (Frey, 1963). He later became the first chairman of the department of zoology, the first director of the Wisconsin Geological and Natural History Survey, and eventually, president of the University of Wisconsin.

Besides the newness of the institutions and the opportunities for capable people, most of the settlers of midwestern states had an interest in and a respect for education that led to the rapid development of their institutions of higher learning. In contrast to the antiintellectualism of the South and the conservatism of the East, the societies of these new states experienced a ferment of new ideas and approaches.[4] Most important for this story, they emphasized an interaction between academic research and the solving of applied problems, an emphasis that meant that the emerging sciences of ecology and limnology had practical challenges to solve, that students and professors had opportunities for employment in applied ecology, and that ecologists could be coupled to the practical needs of their societies. These conditions created vigor in both ecology and limnology.

In northern Europe in a similar landscape, where glacial lakes were abundant, German limnology also developed actively. This growth was part of the rapid expansion of German science and technology in the nineteenth and early twentieth century, which was a result of the creation of the German empire from the German states and the industrialization of the empire. According to William Carr (1969), Germany was the leading industrial nation in Europe by 1900. After 1870, the emphasis of industrial development shifted from coal, iron, and heavy engineering to steel, chemicals, electrical engineering, and shipping. By 1913 Germany's share of world trade nearly equaled that of Britain and was twice that of France. This development was due partly to factors such as rapid population growth, high mobility from rural to urban regions, abundant raw materials, adequate bank credit, assistance from the state in the form of tariffs and subsidies, excellent management, and a skilled working class. In addition, German industrial development rested on scientific research and technological advances, including the invention of the electrical dynamo, synthetic dyes, and the process for making synthetic ammonia. Research, in turn, rested on an academic tradition in the many universities scattered throughout the German states and other German-speaking parts of Europe.

Established in 1891, the biological station at Plon, Holstein, northern Germany, became a center for German aquatic studies (Elster, 1974). August Thienemann (1882–1960) became the director of the Hydrobiologische Anstalt der Kaiser Wilhelm Gesellschaft, which replaced the station, in 1917. The influential technical journal *Archiv für Hydrobiologie* was published by the station beginning in 1916, and in 1925 Thienemann began another publishing

program, *Der Binnengewasser Mitteleuropas*. These German activities were complemented by other work in Northern Europe, notably in Sweden, at Lund under Einer Naumann, and in Russia.

The significance of these North American and European limnological studies to ecosystem science stems from the fact that a lake is a relatively easily defined and discrete object. Thienemann and his colleagues made it clear that limnology studied lakes as whole systems in which the parts interacted to create the system. Although this concept is abstract on land, where the interactions are frequently separated in time and the vegetation dominates the system, in fresh water living organisms are relatively small in size and their life span short, so there is a much clearer linkage between living and physical-chemical processes.

The clarity of system boundaries and processes led Thienemann to a synthetic view of both limnology and ecology. In 1925 in *Der Binnengewasser der Mitteleuropas,* he stated:

> Here the biological and physiological sides of the conographic step toward uniformity come together in a real limnological synthesis. The whole life of waters is considered; the development of life in the water is conceived as a limnological unit of higher order. These units come about through a mutual exchange between biotope and biocoenosis, both standing in functional relationships, one to the other. The character of the living community is limited by its habitat, but it can also change through stability of the biotope, which may be rhythmical or cyclical so that the community returns to its normal condition only at intervals or of long duration when the community can persist.[5] . . .
>
> Each lake can be a living unity, therefore, each case is related to another. They are a microcosm, and therefore, this is the place to discover a higher structure of limnology, an organism of higher order whose organs interact in close mutual exchange. The lake is, we see, a limnological uniformity of the biotope and biocoenosis, of habitat and biotic community. This unity comes through the matter cycles in the relatively closed biotope of the lake. The question then is to characterize these uniformities of individual lakes by their species relationships and to group them together to form a system. These systems are self-standing in nature, considering all their essential characteristics. This shows that they are almost closed. (Thienemann, 1925, 187, 196)

In this article, Thienemann discussed several of the points I introduced in chapter 2. He was concerned about a synthetic view of a lake—realized through the interaction of the biota and its environment—as a system. Thienemann visualized this system as an organism of higher order, in the same way that Clem-

ents had viewed vegetation as a complex organism. In this excerpt, Thienemann refers to the biotic community as the *biocenosis,* a term invented by Karl Möbius, a professor of zoology at Kiel, Germany, in 1877, for the community of organisms growing on an oyster reef. Thienemann's term *biotope* refers to the environmental factors associated with the habitat of the biocenosis.

Thienemann's limnological experience led him in 1939 to express his concept of ecology in sixty numbered paragraphs in "Characteristics of General Ecology" (Grundzuge einer allgemeinen Ökologie). In this important article, he developed a clear statement of the interaction between living and nonliving elements that creates something larger or of higher order: "All separate factors in a biotope interact within the whole life space through mutual exchange. Here their totality works as an organizing factor—a local unit factor for a single biotope (Friederichs), or as a holocoen (Friederichs) for the total living space (or connected world)" (para. 18). In this quotation he used Friederichs's concept of holocoen to express the idea of ecosystem.[6] *Holocoen* and *ecosystem* are synonyms.

Thienemann was conscious of the role of chance in these systems and the flexible and variable nature of equilibrium:

> 30. The basic fact of the biocenotic equilibrium shows us clearly what the true nature of the biocoenosis is. One understands the term "life unit" to mean every life system in which organisms exist. This means that the biocoenosis is the higher order life unit for the single organism. If you call the life unit an organism of higher order, the purpose is only to draw a picture of it (to form a concept of it). Friederichs calls such biological whole bodies in which only single properties of an organism can be measured, biological "organizations," in analogy with organisms, but he stresses the point that there is no identity between them.
>
> In this sense the biocoenosis is an organization. Up to this point of time the organizations are not organisms, but the comparison is very helpful for science and research (Friederichs).
>
> The community is not only an aggregate or sum of organisms (and external factors coexisting in the same habitat) but a whole or system of organisms. The properties of the whole are not equal to the properties of its members. The single members retain properties of the whole which they do not lose if they become detached from the whole (Alverdes).

These conceptual statements place Thienemann in a group of holistic philosophers such as Smuts, Whitehead, and Meyer-Abich and the biologists Clements, Phillips, Friederichs, Weber, and Woltereck.[7] Elster (1974) in his

history of limnology, commented that these ideas of Thienemann echoed Goethe[8] and other earlier cultural figures of Germany. In other words, we might label Thienemann, like Clements, a holistic materialist. He reasoned from his scientific studies of individual lakes toward an abstraction, the whole lake system.

Thienemann's ideas, however, were rejected totally by the empiricists, such as the leading experimental biologist, Max Hartmann, who in his influential book *Allgemeine Biologie* did not even mention ecology. Limnologists, just as plant ecologists, were having difficulty in defining and describing ecological systems in ways that linked the processes in them with the processes studied by physiologists and geneticists. Reductionistic studies in ecology, being based within biology, almost always focused on the finer description of species abundance and distribution within the habitat. Ecological reduction depended largely on taxonomic skills, and those demands almost always resulted in narrowing the field of study, leading the ecologist away from a broad understanding of ecological systems. The compilation of lists of the presence and abundance of species was not considered modern biology. Yet where the limnologist and ecologist could link through chemical processes, the biota, and the environment, a synthetic perspective was possible. Successful synthesis, however, had its own temptation, leading to speculation about the hierarchies of systems. When these abstractions lost their connection to the observational facts, they were also viewed critically by conventional biologists, such as Hartmann. Thus, ecology and limnology were positioned on an arête between two dangerous canyons—one dangerous because it led to an interminable argument over the taxonomic status and abundance of species, the other equally dangerous because it might lead to arid speculation about abstractions that could not be tested by observation or experimentation. These dangers were present everywhere but in Germany, where, possibly more than in other European countries, there were strong cultural supports for the holistic, integrative style of thinking expressed by limnologists such as Thienemann.

The Study of Lakes

Lake biologists began their studies with inventories of the biological organisms in lake water, on shore, and on lake bottoms. The operation was not a simple one, because many of the organisms were microscopic and special sampling methods had to be invented to sample aquatic habitats from boats, piers, and floating platforms. Victor Hensen (1887), an oceanographer, introduced the word *plankton* to refer to the smaller organisms in water and also devised quantitative methods to study them (Elster, 1974). A plankton net pulled

through the water behind a boat collected a variety of animals and sampled a defined volume of water.

Of course, fish had been netted for centuries by people fishing and commercial methods of collecting fish needed only standardization and evaluation to be used to sample this part of the lake biota. The study of the fauna of the sediments was another matter entirely. As mentioned, Möbius had described the bottom organisms on an oyster reef as a biocenosis,[9] and his ideas were readily extended to lakes. The problem, however, was the collection of consistent samples of a bottom made of hard sediments or rocks. Eventually, effective dredges were constructed. Thienemann focused on the fauna of the bottom or the profundal zone, on what is now called the *benthic fauna*. In these structural studies the emphasis was on describing the numerical abundance of the species and changes in their distribution and abundance over time.

Besides descriptive studies of lake biology, the early limnologists were also concerned with describing the lake environment and reasoning from environmental change to biological change. Hermann Weber (1939a, 1939b) had developed his concept of *Umwelt,* or environment, in general biology as meaning not just the interaction between the organism and an environmental stimulus but as including all the factors necessary for the maintenance of the organism. The limnologists approached environment in this broad way. For example, patterns of water temperature with water depth were known at about the turn of the century. Birge and his associate Chancey Juday recognized that temperature caused the stratification of the water into layers, and that these layers were a central feature controlling the distribution and abundance of lake biota. Birge coined the terms *epilimnion* and *hypolimnion* to refer to the upper and lower layers of lake water separated by a layer where the temperature changed rapidly, called the *thermocline* (Birge, 1910).

Temperature stratification interacted with lake chemistry, especially with the dynamics of oxygen. Thienemann, Birge, Juday, and others showed that the distribution of organisms was related to the amount of oxygen in the water (Birge and Juday, 1911). In the profundal zone, after the lake stratifies, the living organisms are dependent upon the oxygen within the hypolimnion. As that oxygen is consumed in metabolism, anaerobic conditions may develop and the living organisms that require rich supplies of oxygen (such as fish) can no longer survive. Organic matter also requires oxygen for its decomposition, and large quantities of decomposing organic material can also deplete the oxygen. These various observations led Thienemann (1925) and Naumann (1932) to develop systems of lake classification, in which nutrient rich lakes and nutrient poor lakes formed ends of a continuum of lake types.

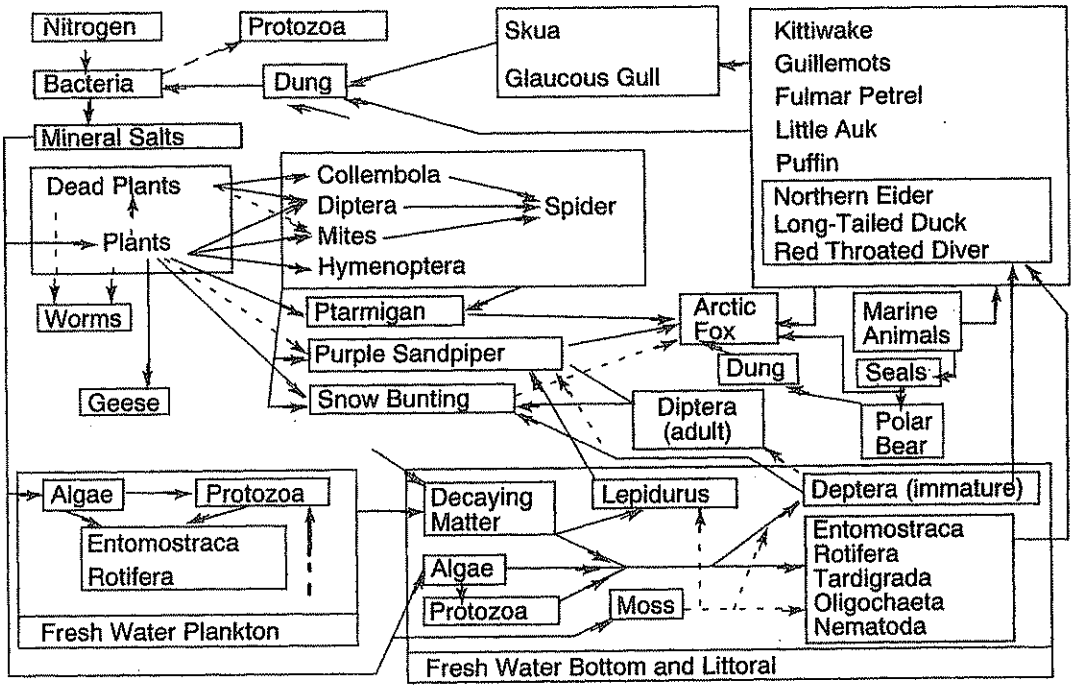
Lake Function

The structural approach to lake ecology satisfied the classical botanist and zoologist in focusing on the collection, identification, and counting of species, but it did not lead to a understanding of the lake as a system. This step required a study of the internal dynamic properties of the lake, what we collectively call its "function." As noted, the functional conception was present in Forbes's concept of the lake as a microcosm, as well as in Möbius's concept of the biocenosis. Nonetheless, it was difficult to implement these concepts until adequate technology was developed to enable the scientist to collect samples at a desired location repeatedly, thereby accumulating enough biological, physical, and chemical data to make functional comparisons and formulate and test hypotheses.

Forbes's (1887) point that the lake system is characterized by the cycling of matter and the building up and tearing down of life through the struggle for existence presented the essence of an agenda for the study of lake function. Cycling and building up and tearing down are different sides of the same coin. Building up protoplasm requires energy to drive the process and chemical materials to build the tissues; tearing down releases energy and materials. If one thinks of the living part of the system as linked intimately with the nonliving, then the cycle is the link between them through which materials flow. The problems with implementing this simple idea were that there are many different materials required by living organisms, the chemical transformations are very complex and in many cases poorly known, and life in a single lake is distributed in thousands of species and in millions of individuals. Further, the environmental sources for materials are complicated. In a lake the sources involve the water and sediments distributed in a variety of zones and layers.

One way through this tangle was to focus on a process central to understanding the dynamics of the entire lake. The process chosen was productivity. Not all ecologists agree on the definition of the terms *production, productivity,* and *product.* At a formative meeting of the International Biological Program in Poland in 1966, I recall three long evening discussions by an international group of ecologists where the meanings of these terms were debated from the viewpoint of different national languages. In Russian, productivity implies fruitfulness or potential and production implies the increase in the biomass over a given interval of time (Ivlev, 1945). Product is then the final phase of a given process. In English, productivity is the rate process, production is the general process, and product is the yield. In scientific reports written in the English language, the latter definitions have been used most commonly.

The production biology approach also made possible a quantitative de-



3.1 The nitrogen cycle on the arctic island, Bear Island, showing the web of interconnected organisms through feeding relationships (Summerhayes and Elton, 1923)

scription of transfers through the food web of the system, an idea grasped by naturalists as far back as Gilbert White of Selborn in 1789. Individuals in the biocenosis feed upon one another in intricate relationships, which, if drawn on a map, convey the impression of a web (fig. 3.1). The web metaphor implies that there is a symmetric order to feeding relationships. Charles Elton, who presented these ideas in a particularly clear way in 1927, used the terms *food chain* and *food cycle* to express them.[10]

In production biology it is necessary to determine the number of organisms in an area, their rates of reproduction and growth, their food requirements and the amount of food consumed, their excretion rates, metabolic rates, and the rate of death. With these data, one can develop a detailed cost accounting for the flow of energy or a chemical element into and out of a population. Richard Weigert pointed out in his 1976 survey of the history of ecological energetics that studies of this type were made as early as 1920 by Eikiti Hiratsuka for the silkworm in Japan. In a field situation it is more difficult to measure each parameter directly, but it can be done. For example, in studying the profundal of Lake Beloie, USSR, in 1939, E. V. Borutsky determined the growth and abundance of each instar of the dominant species, egg laying, emergence, migration in the lake, and losses through predation and death.

These data were put into a diagram showing the biomass dry weight changes for different lake depths during one annual cycle. The species were summed to give a picture of the dynamic behavior of the entire profundal zone.

This type of study is exceptionally detailed, and the data requirements quickly become insurmountable. In this age of computers, it is difficult to appreciate the problems posed when ecologists were obliged to account for the daily changes of individuals of myriad species on sheets of paper, using a pencil and slide rule. The studies such as those of Borutsky, Thienemann, Naumann, Birge, and Juday are astonishing in the amount of detailed handwork they required. The twin forces of difficult data manipulation and the urge to see the whole system led limnologists to group organisms into categories.

Actually, this step was logical as well as methodological because in many groups there is one dominant organism with many rare or subordinate species associated with it, and the dominant species can be used as a surrogate for the others. A simple way to organize these relationships was recognized early by naturalists. Plants were distinguished from animals, and animals were subdivided into herbivores and predators. Elton organized his food chains into a pyramid of numbers partly on this division. He said, "The small herbivorous animals which form the key-industries in the community are able to increase at a very high rate (chiefly by virtue of their small size) and are therefore able to provide a large margin of numbers over and above that which would be necessary to maintain their population in the absence of enemies. This margin supports the carnivores, which are larger in size and fewer in numbers" (Elton, 1939, 69). A few years later, Thienemann (1939) in *General Ecology* added one more category, "The three large groups of living organisms are the producers—the green plants, that use sun energy to build organic from inorganic substances—, the consumer—the animals that build their bodies from organic substances and consume to maintain their life-, and the reducers—the bacteria (and fungi) that are mineralizers, reducing the complex organic matter into the elementary composition" (Thienemann, 1939, 268–69).

The structured division into producers, consumers—which are subdivided into herbivores and carnivores—and reducers gives a simple organization to the complex biocenosis. For some, such as the Russian V. S. Ivlev (1945), this classification was too simple. He complained that the peculiar and important feeding habits of species and individuals were ignored by grouping organisms into a few categories. This criticism has been echoed by biologists ever since, but the seductively simple plans of Elton, Thienemann, and others and the urge to make the ecosystem concept quantitative led ecologists to overlook or ignore it.

Equilibrium

Studies of complex structures and functions would also be made easier if the patterns of nature were regular or stabile. *Equilibrium, balance,* and *stability* are all terms that imply constancy over time, predictability, and "unchangingness." The clocklike universe of the eighteenth-century imagination had this sort of predictability in it. It was thought that the planets moved in unchanging orbits and that nature was organized in a great chain of being that defined the place of every living creature. The only problem with this model is that our own experience shows that nature is constantly changing. We are surrounded by changing seasons, growing and developing plants and animals, and we age and become more experienced ourselves. Nevertheless, science in the nineteenth century seemed to support the idea that there was an underlying stability in the universe. Physicists showed that energy transformations followed laws that permitted determination of the thermal and mechanical properties of a body of uniform composition. Later, Tansley advanced his ecosystem concept based on his interpretation of these physical equilibria.

In 1878 the American physicist Josiah Willard Gibbs published his epochal monograph "On the Equilibrium of Heterogeneous Substances," which opened up the field of chemical equilibria and established the field of physical chemistry. Scientists grew increasing aware of the operational analogies between organic and inorganic matter; the difference between living and nonliving matter was that living organisms were in a state of dynamic equilibrium and nonliving matter was in a state of static equilibrium. The French physiologist Claude Bernard founded the science of physiology on a theory of equilibrium—the idea of the constancy of the internal environment of the body. Walter B. Cannon later coined the word *homeostasis* for this characteristic stability. It is not surprising that ecologists such as Clements and Forbes adapted these ideas and applied them to the objects they studied. The same process was occurring in the social sciences (Russett, 1966).

The problem for the student of lakes was to demonstrate a condition of equilibrium. Here there was a central problem in ecology, a problem I call a "confusion of levels." If we consider a lake as an object of interest, then the equilibrium of the lake involves a dynamic condition of its behavior. Thinking analogically from a individual human being, we would look for constancy in its health or well-being, its work capacity, and the stability of its personality. What is the health, work, and personality of a lake? Since most ecologists are trained as biologists, the answer to this question is almost always framed in terms of the biological elements of the system. These elements are the most dynamic and are responsive in a way different from the physical-chemical factors of the environment. Yet, the system is the interaction of living and nonliving matter within

the lake basin. One way the behavior of a lake may be defined is through its conversion of input water from streams and overland flow into the output water of its draining river. This definition emphasizes the point that the behavior of the system reflects the system as a whole, not just a single component. We confuse levels if we judge the performance of the whole—the lake—solely by the performance of a component—the biota.

In this period, ecologists could do little more than advance the hypotheses that there were systems and that they displayed equilibrium conditions. It was not until many years later that it was possible to describe the behavior of systems directly and determine if the behavior was constant over time.

Thus, Forbes's assertions about lakes as microcosms were only partly capable of being verified. By the 1940s, however, biologists were building an understanding of the dynamic behavior of parts of lakes: the profundal, the plankton, the fish, and the littoral plants. Could these partial studies be put together to form a functional description of a whole lake?

THE LAKE AS A SYSTEM

Juday and Lake Mendota

Chancey Juday (1871–1944), professor at the University of Wisconsin, was among the first to attempt a functional description of a whole lake. His summary was based on extensive research by a team of investigators at the university who, with Birge, had studied Lake Mendota and other Wisconsin lakes since 1895. Juday (1940, 439) chose to present his whole lake assessment in the form of an energy budget. He said that "the annual energy budget of a lake may be regarded as comprising the energy received from the sun and sky each year and the expenditures or uses which the lake makes of this annual income of radiation. In general the annual income and outgo substantially balance each other." This idea was an exceptionally important one because it gave ecologists a theoretical structure that would show if an energy analysis was complete. According to the laws of thermodynamics, energy input and output must balance. If they do not, it means that some processes were missed in the analysis or that the measurements were faulty. Juday considered the physical heat budget of the lake, through which most energy flows, as separate from the biological budget. The physical heat budget involved solar radiation, melting ice, the heat produced by the water and the bottom, evaporation, and reflection. The biological budget involved the energy converted by photosynthesis and its use by each organism.

These Wisconsin scientists had data collected month by month, year by year, at a level of detail unlike that of any other group. For the biological

budget, it was necessary to have information on the energy uptake and loss of the plankton, bottom flora and fauna, and the fish. Juday recognized the existence of food chains, where energy was transferred from aquatic plants to a series of animal populations, but he did not develop this picture. Rather, he limited himself to a comparison of the energy conversion through photosynthesis and its transfer to animals. Even so, Juday found it necessary to make several extrapolations and assumptions. He did not know the production of the plankton, which consisted of many different populations with different life cycles. Therefore he estimated the annual production of the plankton from an average turnover rate of the organic matter in the mean standing crop of plankton. Juday's willingness to group data for species and to extrapolate from these data to the whole system anticipated an approach common in later studies.

The main point drawn from this attempt at system analysis was that the energy flowing through the biota was an extremely small amount of the total budget. Juday found that the biota used about 1 percent of the total input. Of the energy collected through photosynthesis, about 5 grams of plant food were required to produce 1 gram of animal. The major part of the energy budget was in the physical processes of the lake, a subject in which the Wisconsin researchers had particular interest. These physical processes caused the lake to "take a deep breath" at the time of spring and fall overturn when all the waters of the lake were mixed. Birge (1907) had earlier used the metaphor "the lake respires," to draw attention to this phenomenon.

It is doubtful that Juday's attempt at total system description was satisfying to many biologists of the day. The role of the biota was insignificant in terms of system energetics, and it was necessary to make too many assumptions and ignore too many observable behaviors of the biota to calculate the energy intake and loss of groups of organisms, such as plankton. Yet, it is important to note that Juday did not use a holistic philosophy to justify his approach. The lake as an object was an adequate basis for his study. Forty or fifty years of limmnological research had established a foundation for his effort to bring together physical, chemical, and biological studies into a single description of a lake. This was a major advance in ecology, though Juday's effort was soon overshadowed by that of Raymond Lindeman.

Lindeman's Trophic-Dynamic Concept

The story of Raymond Lindeman (1915–42) is documented in a biography by Robert Cook (1977) and a memoir by Charles Reif (1986). He is well known to ecologists because his article "The Trophic Dynamic Aspect of Ecology"

3.2 Raymond Laurel Lindeman at the time he was a graduate student. Photograph provided by Charles Reif

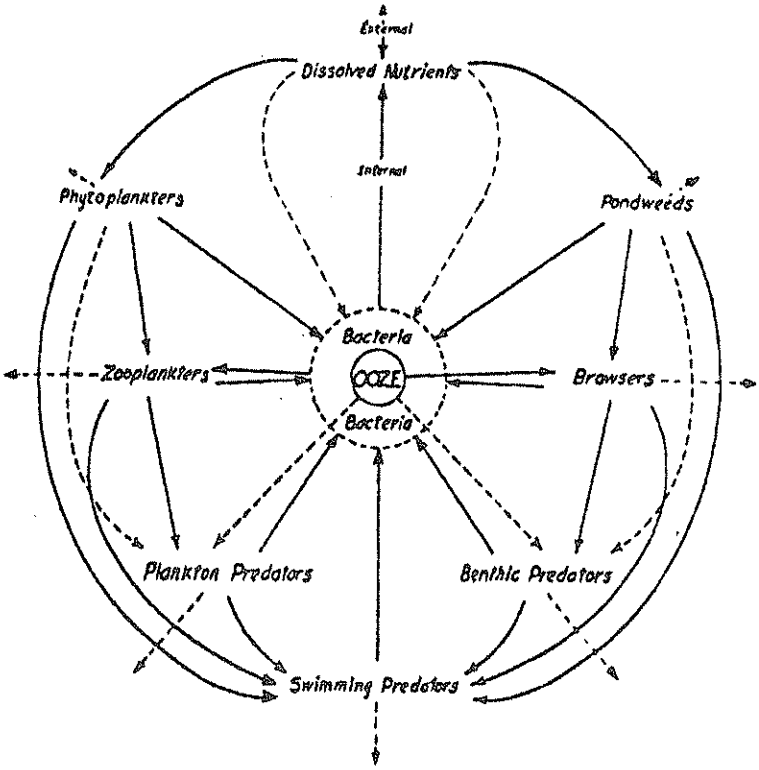
(1942) is an acknowledged classic in the field, mentioned in all the major textbooks and regularly included in the lists of the literature in the field. Lindeman earned his doctorate in the department of zoology at the University of Minnesota, where his professors included Samuel Eddy (zoology) and William S. Cooper (botany), both key figures in American ecology. After graduation, with a Sterling Fellowship from Yale University, he worked with the distinguished limnologist and ecologist G. Evelyn Hutchinson.

Of the six monographs that constitute the Lindeman oeuvre, two are relevant to our story. These are "Seasonal Food Dynamics in a Senescent Lake" (1941b) and "The Trophic-Dynamic Aspect of Ecology," the result of five years of fieldwork on small Cedar Bog Lake near the University of Minnesota. Lindeman and his wife, Eleanor Hall Lindeman, sampled the biota of the lake with plankton nets and bottom dredge throughout the different seasons, as well as the water and bottom sediments, observing the growth, development, and

distribution of the littoral vegetation, vertebrate animals, and the context of the lake in the forest. The study was unusual because it attempted to sample all elements of the biota at the same period of time. In a sense, it replicated the much larger team efforts on Lake Mendota and other Wisconsin lakes by Juday and Birge and on German and Swedish lakes by Thienemann and Naumann. It was necessary that the lake be small and well defined in order for two people to study the whole system. Cedar Bog Lake at the time of Lindeman's study had a depth of 1 meter, an area of 14,480 square meters, and a shoreline of 500 meters.

Lindeman concluded that the lake was an ecosystem. He was the first to implement Tansley's concept explicitly in a quantitative effort to define the system and describe and understand its dynamic behavior. The initial task Lindeman had in implementing the ecosystem concept was to organize an immense amount of data on the biology, distribution, and abundance of the lake plants and animals into a scheme or pattern. His approach, evolved from that of others, was a unique and creative one called the *trophic dynamic aspect*. The first stage in building the trophic-dynamic approach was derived from prior studies by Möbius (1877), Forbes (1887), Forel (1907), Shelford (1918), Alsterberg (1922, 1925), Thienemann (1926), and Strom (1928), who had suggested that the biota could be described as a network of interactions with groups of organisms linked by feeding. Lindeman created his scheme to emphasize the special character of Cedar Bog Lake. He placed *ooze,* or the material that filled the bottom of the lake at the center of the diagram, surrounded by two different flow patterns (fig. 3.3). One set of linkages was based on plankton and the other on littoral pond weeds. All parts of the biota were linked to the ooze. By constructing the diagram in this way, Lindeman emphasized the interaction of the living and nonliving parts of the lake, which were intimately interconnected. Lindeman's diagram was similar, in his emphasis on the ooze, to those of Thienemann (1926), Strom (1928), Rawson (1930), and Wasmund (1930), all of which were illustrated and discussed in his thesis. We can assume that his diagram was a central element for his organization of information on Cedar Bog Lake, since he published the diagram in each of his major publications.

His second task involved formulating a way to go beyond earlier attempts to describe lake metabolism and energy flow, which Lindeman called the *dynamic species distribution approach*. He solved this problem by focusing on the food cycle within the ecosystem, whereby he could link the living and nonliving parts of the system and organize species into groups based on their food habits. He identified species, determined their food habits from observation, experiment, or the literature, and then organized the various species into food groups. The food groups became the cells of his ecosystem diagram. Feeding



3.3 Lindeman's diagram of a food cycle in Cedar Bog Lake (Lindeman, 1941b). Published with permission of the *American Midland Naturalist*

was made comparable between diverse biotic groups by converting food into energy units.

Finally, Lindeman used this new trophic-dynamic approach to understand ecological succession. The successional paradigm must have been of special interest to him because one of his professors, William Cooper, was a major contributor to the scientific study of successional.[11] Cedar Bog Lake was a senescent lake, formed by a melting ice block after the retreat of glaciation, which by the 1940s had reached a point where it was nearly filled with peat and marl. The lake was primarily understood as a stage in lake succession, an imbalance between the forces of production and catabolism. Plant organic material gradually increased and changed the depth and quality of the lake. Lindeman's aim was to use the trophic-dynamic approach to understand the balance between these processes.

In 1939, Lindeman met Edward S. Deevey, a former student of Hutchinson, at a hydrobiology meeting at Columbus, Ohio, and found that they had common interests. Deevey had studied the biological history of lakes by sediment core analysis, and he and Hutchinson were interested in lake succession. It

was Deevey's suggestion that led Lindeman to apply for a fellowship at Yale to work with Hutchinson following his graduation in March 1941. The move was important in his interpretation of the data he and his wife had collected on Cedar Bog Lake. In the meantime, his article on the seasonal dynamics of a senescent lake, which contained most of the biological data from his thesis, was accepted for publication in the *American Midland Naturalist*.

The major portion of the seasonal dynamics treatise recounts the abundance, biomass, and feeding relationships of the biota, organized into the categories of the food cycle diagram. The dominant species in each group were reported in detail and in some cases were surrogates for other, less abundant or less well known species. Lindeman found great variation among these species. From one year to the next the dominant groups or the species within a group differed widely. He explained this variation as being caused partly by factors external to the lake, such as water inflow, rainfall, winter temperature, ice cover, and chemical flux.

He moved beyond his thesis into three new perspectives. First, the biomass of the species were converted to energy units, using the conversion factors determined by Birge and Juday for Lake Mendota.[12] In the thesis, the figure that reported the biomass dynamics of food groups was converted to energy by altering the abscissa of the figure, using the conversion factor of 10 grams centrifuged wet weight per square meter as equal to one calorie per square centimeter. Second, the annual production of the food groups, calculated by assuming appropriate turnover rates for each group—following the approach of Juday for Lake Mendota—were summed and presented as three trophic groups: producers, primary consumers, and secondary consumers. Third, efficiencies of transfer between groups were calculated by comparing the amount of energy in annual production in various food and trophic groups. For example, about 10 percent of the production of the producers was in the production of primary consumers, and about 19 percent of that in secondary consumers compared to that of the primary consumers.

These important advances in theory were a natural extension of Lindeman's thesis, obtained by applying an energetic approach to biomass, following the lead of Juday. Energy was a key part of metabolic physiology, recognized as central by other ecologists, but not yet readily applied to the metabolism of ecological systems. Lindeman had more detailed and concentrated information than Juday. By applying energetics to his standing crop data, he could extend Juday's approach into a more detailed description and expansion of the concept of ratios or efficiencies. Possibly, there was also encouragement from Hutchinson and Deevey,[13] who used ratios of species remains in sediment cores to demonstrate patterns of change over depth.

In his thesis, the energetic approach was based partly on an article by Edward Haskell (1940), in which Haskell attempted to create a physical mathematical theory of ecology. Haskell characterized the environment as entropic in nature, plants as regions of integrated entropic and biocatalytic processes, and animals as entropic, biocatalytic, and signalloid processes, and proposed that each might be described by differential equations of sequentially higher order. Hutchinson (Cook, 1977) said that he did not believe half of Haskell's propositions, and Lindeman did not reference Haskell in his published papers, since the theoretical underpinning for trophic dynamics was no longer necessary.

The organization of the food groups recognized in his trophic diagram into trophic levels was also a natural step, since Thienemann (1926) and other limnologists had used categories of producers, consumers, and reducers to organize biological data. Yet Lindeman was faced with an exceptionally varied fauna and flora that changed dominance each year. It was easier to organize these alternating species into groups that represented their collective feeding relationships than to keep them separate as biological units. In this way he could discuss components of ecosystems that had continuity year to year and season to season.

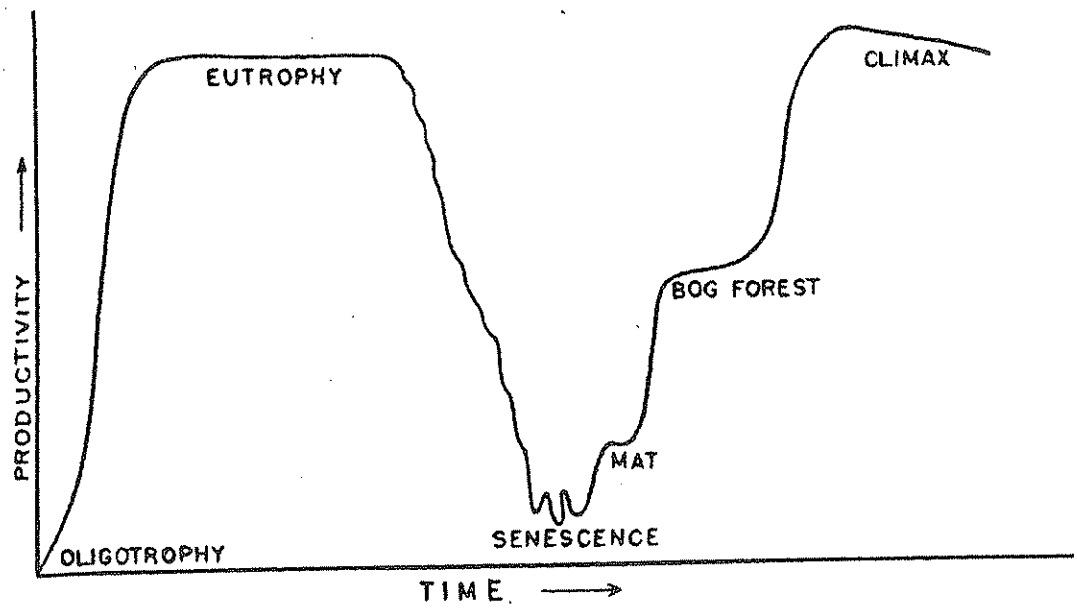
"The Trophic Dynamic Aspect of Ecology" was based on the final chapter in his thesis, "Cedar Bog Lake: The Ecosystem or the Trophic Dynamic-Viewpoint in Ecology." The article was started in February 1941 but after he moved to Yale in September, it became dramatically altered, incorporating ideas provided by Hutchinson, who had arrived at some of Lindeman's conclusions independently.[14] Still, this draft was rejected when it was submitted to *Ecology*. Cook (1977) tells us that the referees were two of the most distinguished American limnologists, Juday and Paul Welch of the University of Michigan. Both based their rejection on the theoretical nature of the article, asserting that it was premature and based on too particular a lake.[15] The reviewers also thought that a theoretical article was inappropriate for *Ecology*. Although it seems ironic that Juday, who had published on the energetics of Lake Mendota several years before, would reject Lindeman's article, he and Birge were studying 529 lakes in northeastern Wisconsin. Their survey showed how special each lake was and how difficult it was to demonstrate a single-property characteristic for all lakes. Hutchinson appealed to *Ecology*'s editor, Thomas Park, of Chicago, strongly supporting the need for theoretical monographs in the journal of the Ecological Society of America and taking responsibility for some of the ideas expressed in the article.[16] Park offered to consider a further revision. When the fourth draft was submitted in March 1942, Park sent it to another distinguished ecologist, W. C. Allee, of Chicago, who gave it lukewarm approval. Park, on his own decision, accepted the article, and it was

published in October 1942, after Raymond Lindeman had died. The article was published with a generous addendum by Hutchinson.[17]

A comparison of the finished article to the final thesis chapter shows how far Lindeman's thinking had advanced. The format of both are similar, with sections on definitions and concepts, followed by the dynamics of ecosystems, and concluding with the application of trophic dynamics to ecological succession. The concept section in his article asserted that the ecosystem was the key concept to understanding Cedar Bog Lake because it involved the interaction of living and nonliving parts of the system. The ecosystem dynamics section in his thesis was, as mentioned earlier, based on Haskell's (1940) idea of extending physical and mathematical ideas to ecology. Lindeman admitted that he did not know how to implement Haskell's concepts. Instead, he turned to productivity (defined as the amount produced per unit of time) to organize the static data on species biomass and numbers and attempted to explain a change in productivity by the change in the nutrient supply required to build the biomass and by external factors, such as rainfall that raised or lowered the lake level. In the article, Haskell's ideas were dropped in favor of a symbology derived from Hutchinson, where each trophic group was represented by the difference in the rate of energy entering or leaving the group. In this scheme, productivity was defined as the transfer between trophic groups, with emphasis on comparisons using ratios and efficiencies. Productivity was corrected to account for losses from metabolism, predation, and decomposition. Lindeman found a progressive change in efficiency up or down the trophic sequence. For example, the efficiency of transfer appears to increase as one moves from producers to tertiary consumers. This section in the treatise is so fundamentally changed from Lindeman's thesis that it is entirely new, except for carrying over the concept of trophic groups or levels.

The final portion of his thesis represented his argument about understanding trophic dynamics in the context of ecological succession, which shifted in the article to a focus on trophic dynamics to explain succession as ecosystem development. Lindeman accepted conventional theories of ecological succession in general, and of lake succession in particular. These included the theories of Clements that succession is a process leading to an equilibrium state set by the regional climate and of Thienemann and other limnologists that lake succession is a process that begins with oligotrophy, where production is limited by a low nutrient supply, progresses to a eutrophic state—where production operates at a high level of activity—and eventually, as the lake fills in, becomes a terrestrial bog and finally a forest.

When Lindeman compared his data from Cedar Bog Lake with those for other lakes, for example, the energy production with that of Lake Mendota and



3.4 Lindeman's hypothetical relationship of productivity changes over time in a deep lake, which eventually, following the theory of Clements, would become a climax forest (Lindeman, 1942, 413). Published with permission of the Ecological Society of America

the process of deposition with that of Linsley Pond, Connecticut, he found that Cedar Bog Lake was not, as he had earlier thought and remarked on in the thesis, highly productive. Lake Mendota producers were about four times as productive as those in Cedar Bog Lake. In his article, Lindeman separated Cedar Bog Lake from other lakes and drew a new curve of productivity and time (fig. 3.4), showing a long period of stable productivity, followed by a decline to senescence, then an increase as terrestrial systems developed and covered the former lake bed.

In his summary, two conclusions came from his thesis and three were new. The two from the thesis were that the ecosystem was the fundamental unit of trophic-dynamics and that the pond can be organized into trophic levels. A further conclusion was derived from the thesis but was not stated explicitly. This conclusion was that the more remote the level was from the source of energy, the less dependent it was on one source. The new concepts stated that the energy of the contributing level *a* is greater than that of the receiving level *b*, that respiratory loss is higher at the higher trophic levels, and that consumers at the higher levels are more efficient in energy transfer than those at lower levels. His two final conclusions referred to succession, that productivity and efficiency increase in early succession and that consumer efficiencies increase during succession.

Lindeman's trophic dynamic treatise implemented the ecosystem concept. Further, it showed that a single individual, with a helper, could study an entire ecosystem and describe the activities of the biota in an acceptable fashion. It was within the ability of a single investigator to study a small lake, spring, or pond,[18] while a team was required to study a large system, such as Lake Mendota. From a theoretical view, it demonstrated that one could identify an object in a physical environment, defined by the morphometric boundaries of the depression, and study it as a system. This system had a structure of living species and nonliving material. It also had a metabolism and converted input energy from the sun into heat energy or energy stored in sediments and ooze. It received nutrients from its basin, recycled them through the biota and nonliving materials, and exported them in water, atmospheric gases, pupating insects, and food for terrestrial animals. Finally, the lake ecosystem had a development pattern. It changed through time. This change, called succession, was a function of the interactions of the biota and nonliving material with the external climate, nutrients, and human disturbance. Lindeman focused on the first and last point; he did not develop the theme of nutrient cycles. To complete the story I briefly consider this theme.

A Supporting Theme

Lindeman introduced the concept of the food cycle in his writings. The phrase was taken directly from Thienemann's *Der Nahrungskreislauf,* but Thienemann did not develop or fully implement the concept in its trophic-dynamic aspect. The concept includes the idea that nutrients enter and leave a system through transport mechanisms in the atmosphere, hydrosphere, and biosphere, and that living organisms within the system, which are actually subcomponents of the ecosystem, take up, store, and release nutrient elements to their environment. In this way the living part is coupled to the nonliving part of the system, which functions alternately as a source or sink of elements.

The concept of nutrient cycling enters ecology from several sources. The first is geochemistry, which focuses on the chemical flows between the biota, atmosphere, hydrosphere, and lithosphere (Fortescue, 1992). Geochemical studies began about the same time as ecological work. The pioneer American geochemist F. W. Clarke had published a summary of geochemical data in *The Bulletin of the U.S. Geological Survey* in 1908. To understand the linkage of living and nonliving parts of the ecosystem, the chemistry of the environment had to be integrated with biology. This process of integration was undertaken by several individuals. The first was Vladimir Vernadsky (1863–1945), a Russian, who developed the concept of biogeochemistry. Vernadsky was basically a min-

eralogist (his doctoral thesis was "The Phenomena of Crazing in Crystalline Matter"), but he was active in many areas of science, science management, and social matters. During his stay at the Sorbonne in 1923–26, he wrote on geochemistry, mineralogy, crystallography, biochemistry, marine chemistry, the evolution of life, geochemical activity, and futurology (Baladin, 1982). Rudolf Baladin (1982, 41–42) comments, "His capacity for work was amazing. Up to his very old age he worked 10–12 hours a day, and sometimes even longer, combining a consistent sharp interest in investigations with the rigid organization of his work."

Vernadsky merged the data from several fields into one perspective that considered the earth as a chemical system where the elements cycled between the various parts. His perspective had a strong influence within the Soviet Union, where he was recognized as a scientific leader (he organized the first national scientific academy, the Ukrainian Academy of Science, and was its first president immediately after the civil war), and was also recognized throughout the world through his lectures, travels, and books. His book, *The Biosphere,* first published in 1926 in Leningrad and in 1929 in French as *La Biosphere,* had wide impact as a scientific expression of a global system of man and nature, which was an antidote to the virulent nationalism that was being expressed at the time, especially in Europe.

Vernadsky's student A. E. Fersman (1883–1945) formulated methods to map geochemical provinces, thus creating a spatial component in the field. Another pioneer was the Norwegian V. M. Goldschmidt (1888–1947), who emphasized the integration of geochemical cycles. All these pioneers were chemical holists in that they were concerned with the movements of all elements in the biota and environmental spheres.

Fortescue also discusses in his history of landscape geochemistry the Russian school of soil science and geography of V. V. Dokuchaev (1846–1903). Two of Dokuchaev's ideas that are relevant to the ecosystem concept are that every natural zone constitutes a regular, natural complex in which living and nonliving aspects of nature are closely associated, and that soil is an independent natural body that must not be mistaken for surface rocks. These ideas were at the heart of Dokuchaev's thinking and provided a base for the organization of the science of landscape geochemistry.

Another contributor to the concept of nutrient cycling was an American, Alfred Lotka (1880–1949). Lotka was born in Europe of American parents and educated in Germany, France, and England. He was a physical chemist and for much of his life worked in industry and government. His scientific work was done in his spare time, published in a variety of scientific journals, but was largely unrecognized. Sharon Kingsland (1985, 29) describes his work: "Lotka

labored on, building his program piece by piece; but he was like a mole, anxious to soar yet equipped only to tunnel deeper underground. His schemes and scratches had brought him no closer to recognition by 1920, when his small movements caught the eye of an eagle, which swooped down to raise him up in its large but friendly talons. The eagle was Raymond Pearl of the Johns Hopkins University." Pearl was professor of biometry and vital statistics in the new School of Hygiene and Public Health, and he offered assistance to Lotka. Lotka moved to Baltimore in 1922 and began writing *Elements of Physical Biology,* in which he viewed the entire earth as a single system with the various components linked by exchanges of chemical elements and driven by solar energy. He commented, "We shall probably fare better if we constantly recall that the physical object before us is an undivided system, that the divisions we make therein are more or less arbitrary importations, psychological rather than physical, and as such, are likely to introduce complications into the expression of natural laws operating upon the system as a whole" (p. 158). Lotka anticipated the study of food chains, producers and consumers, cycles of water, nitrogen, carbon and other elements, and the mathematics of trophic transfer. Unfortunately, his book did not stimulate the creation of a new science of physical biology. On the one hand physicists, generally, were not interested in his ideas. On the other hand, some ecologists found the ideas congenial since his systems approach was based on a quantitative database from a wide variety of disciplines, and he implemented at a global level what many, such as Thienemann, Birge, and Juday, were trying to do on a smaller scale. Charles Adams, president of the Ecological Society of America in 1923, recognized the worth of Lotka's book and encouraged him to write a review in *Ecology* (Adams, 1915). He never did, but he did join the society in 1925.

Lotka's book was reprinted in 1956 as *Elements in Mathematical Biology,* and it became an ecological classic that was widely consulted in the 1960s and 1970s. Although it appears to be a precursor to ecosystem ecology, we do not know how many ecologists were familiar with the first edition of Lotka's book. It is not cited in the literature that defines the developments we have discussed, but some ecologists, other than C. C. Adams, may have been influenced by it. Now, at the end of the twentieth century, when we are concerned about changes in the global climate, it has, like Vernadsky's writings, a modern feeling.

Ecological studies in biogeochemistry were advanced by the group around Hutchinson of Yale University. Hutchinson played a pivotal role in the story of ecosystem ecology, as well as in American ecology in general. He was born in England and grew up in the academic city of Cambridge. Later, he worked in South Africa before moving to Yale in 1928. Hutchinson was familiar with

Vernadsky's ideas, was a colleague of Vernadsky's son, who was a Yale professor, and translated several of Vernadsky's articles. In the 1930s, Hutchinson and his students began their studies of the element cycles in the small lake Linsley Pond on the outskirts of New Haven.

One of the organizing principles of Hutchinson's theoretical work was the familiar concept of system equilibrium or balance. He thought that systems evidenced processes of self-regulation that produced and maintained equilibrium conditions. As a case in point, Edward Deevey, in his examination of cores of the organic sediments that had accumulated in Linsley Pond since postglaciation, found a period of high productivity followed by a relatively constant rate. Hutchinson interpreted this pattern of productivity as due to modification of the environment by the pond organisms, and forming an ecology of self-regulation leading to equilibrium conditions. Hutchinson's other students examined biogeochemical cycles, productivity, and equilibrium in other systems. Among these was Howard T. Odum, whose thesis concerned the strontium cycle.

The second path to nutrient cycling came from physiology. The German agricultural chemist Justus Liebig is usually cited as the first scientist to recognize that chemical elements were limiting to plant growth (Liebig, 1876). Physiologists concerned about the nutrition of animals and humans or plant growth demonstrated that many of the chemical elements of the periodic table were essential for living organisms. A comparison of the geochemical abundances of elements in the biosphere does not correspond closely with the abundances in the human body (Lotka, 1925), leading to the conclusion that living systems evolved their own unique chemical compositions, which are maintained in a variety of chemical environments.

The selection of essential chemical elements from the environment and the interplay between anabolic and catabolic processes that maintain a steady state or homeostasis provided the ecologist with a conceptual framework that could be applied by analogy to ecological systems. Actual biogeochemical work was initiated by ecologists such as Thienemann and his group at Plon, and G. Evelyn Hutchinson[19] and his students at Yale University.

With Raymond Lindeman we see for the first time a deliberate effort to implement Tansley's ecosystem concept. His focus was on the dynamic processes of the ecosystem. The idiom in which he expressed this process was energy. Lindeman introduced most of the major questions and concepts of modern ecological energetics, including questions about the length of food chains, the efficiency of trophic transfers, the storage of energy at different levels, the rates of primary productivity, the problems of correcting energy

values for losses due to respiration, predation, and decomposition, and the role of bacteria and microorganisms in cycling dead organic matter. In addition, he made clear the idea that ecosystems develop through ecological succession and are tied to the energy dynamics of the system and the concept that nutrient cycling, as food cycling, is linked to the wider biogeochemical cycles coupling one ecosystem with another.

Approximately seven years after the ecosystem concept was introduced, Lindeman had defined an outline for a research program that would occupy ecologists for the next forty or more years. This program asserted that nature is organized into ecological systems that are recognizable objects such as lakes and that have an origin and development leading to a steady state or dynamic equilibrium. These systems have a structure—defined as a network of feeding relationships among their species populations—that can be simplified by grouping the populations into food chains or trophic levels. The ecosystem has a behavior, beyond that of development over time, that involves the processing of energy received from the sun or other systems into heat and work, and the processing of chemical elements imported into the system into various storages and outputs. These are the energy flows and the nutrients cycling between the species populations and between them and the nonliving parts of the system. The structure and the function of the system can be expressed mathematically as a series of equations describing the interactions between system components.

This full program was described in rough terms only in the 1940s because of the difficulties encountered in the study of a whole system in the field and in analysis of the collected data without the help of a computer. Yet the skeleton was clear, it only remained to build up the flesh. This became a possibility after the hiatus imposed on research during the second world war.

A HISTORY OF THE ECOSYSTEM CONCEPT IN ECOLOGY

More Than the Sum of the Parts

Frank Benjamin Golley

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