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Summary. Lindeman's classic paper on energy flow in ecosystems was initially rejected for publication in *Ecology*. Reviewers felt there were insufficient data to support the theoretical model and that theoretical essays were inappropriate for *Ecology*. The paper was subsequently accepted by Thomas Park, the zoological editor, after correspondence with G. Evelyn Hutchinson who indicated the importance of theory in the development of ecology.

In September 1941, Raymond Lindeman and his wife, Eleanor Hall Lindeman, arrived in New Haven to begin work with G. Evelyn Hutchinson, a limnologist teaching at Yale University. With him Lindeman brought the last chapter of his Ph.D. thesis, awarded the previous spring from the University of Minnesota for a 5-year study of the biology of a senescent lake, Cedar Creek Bog (*1*). This chapter underwent several draft revisions and was published posthumously in the journal *Ecology* as "The trophic-dynamic aspect in ecology" (*2*), and it subsequently became the foundation for much future work concerning the dynamic flow of energy in plant and animal communities (*3*). This paper would have formed but another historical fragment in the structure of modern ecological thought were it not for the fact that when first submitted for publication, it was rejected by the editor on the advice of two referees who were prominent limnological ecologists. After a subsequent exchange of letters between Thomas Park, editor, and Hutchinson, a somewhat modified version of the manuscript was accepted. Because of the ecological importance of the work, and the unusual circumstances of its publication, I will recount here the story of its rejection and ultimate acceptance (*4*).

Perhaps the most prominent problem to which ecologists in the early decades of this century addressed themselves was the structural and temporal organization of plant and animal communities. This was particularly true for the underlying ecological processes that determined the patterns of change seen in the distribution of organisms and the succession of species following natural and human disturbance. Lindeman believed that the understanding of ecological succession in lakes over long periods of time depended upon the quantitative assessment of the biological relations of the organisms found in those lakes; and he chose for study the trophic (nutritional) relations of all the inhabitants of a shallow, weedy body of water lying in the transition between late lake succession and early terrestrial succession. For 5 years he and his wife extensively sampled the population of aquatic plants and phytoplankton, the grazing and predatory zooplankton, the benthic fauna of worms and insect larvae, the crustaceans, and the fish; and through this they gained a very intimate understanding of the movement of nutrients from one trophic level to another. To integrate this knowledge of food-cycle dynamics with current principles of community succession, Lindeman created the trophic-dynamic viewpoint presented in the last chapter of his thesis: "The trophic-dynamic viewpoint, to be elaborated in this paper, emphasizes the relationship of energy-availing (food cycle) relationships within the community to the process of succession" (*1*). In essence he was grappling with the problem of time scales and arguing the importance of short-term trophic functioning to an understanding of long-term dynamical changes, this being an integration that he believed was hindered by the terminological distinction between autecology and synecology.

Lindeman's paper begins with a discussion of community concepts; and, drawing on the work of Thienemann and Tansley, he stresses the functional integration of organic and inorganic cycles of nutritive substances: "The ecosystem may be formally defined as the system composed of physical-chemical-biological processes active within a space-time unit of any magnitude, that is, the biotic community plus its abiotic environment. The concept of the ecosystem is believed by the writer to be of fundamental importance in interpreting the data of dynamic ecology."

There follows a lengthy discussion of trophic operations; here the most important intellectual contributions of the paper are created. Quoting from a locally published set of lecture notes by Hutchinson, Lindeman establishes a theoretical model of nutrient cycling expressed explicitly in terms of energy flow symbolized by mathematical equations. He then proceeds to calculate the values of the appropriate terms from his own data and those of others. The analysis of trophic relations in terms of energy leads easily to concepts of biological efficiency, and Lindeman arrives at several very general relations regarding the flow of energy in ecosystems. In the final section of the paper these relations are brought to the analysis of successional development, with particular emphasis on rate-controlling processes and the ecological efficiency of energy transfer over this expanded time scale. It is here that the analogy between the development of an organism to maturity and community changes during succession finds its fullest expression; and it is the elaboration of this metaphor which has provided continuing inspiration to community ecologists (*4a*). Thus, in his effort to integrate ecological patterns of differing temporal scales, Lindeman reduced the trophic relations of a community to a common denominator, energy, and created around this focus a theoretical structure yielding predictions with which future workers could design their own investigations.

The Writing

On 19 March 1941, a year before the acceptance of his paper by *Ecology*, Raymond Laurel Lindeman received his Ph.D. in zoology from the University of

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Minnesota. As part of the completion of the Ph.D. requirements, Lindeman had already submitted the first chapter of his thesis for publication, and it would appear early in 1941 (*5*). He had therefore made the decision to publish the thesis as a series of papers rather than a single monograph, thus separating the great body of collected data (*6*) from the theoretical treatment represented in the trophic-dynamic paper (*7*).

Lindeman was assisted throughout much of the fieldwork and writing of his thesis by his wife, Eleanor, whom he married in 1938 (*8*). In the spring of 1941 they made plans for the examination of sediment cores taken from Cedar Bog Lake with Ray performing chemical spectroscopic analysis and Eleanor identifying diatom microfossils. A year earlier, Ray had met Edward Deevey (*9*) at the hydrobiology meeting at Madison (*10*), who had suggested that Raymond apply for a fellowship to work with Hutchinson at Yale. This he did, and in April 1941 he was awarded a Sterling fellowship for a year. He worked on manuscripts drawn from his thesis through the spring and submitted a large paper on food cycle dynamics which formed the main body of data supporting his general conclusions in the thesis (*6*). The final chapter of his thesis was undergoing revisions and would become the future trophic-dynamic paper.

In late August the Lindemans arrived in New Haven and another revision of the trophic-dynamic paper was immediately begun, stimulated by conversations with Hutchinson and a recently compiled, but not widely circulated, manuscript of Hutchinson entitled "Lecture notes on limnology" (*11*). Manuscript 3 [see (*7*)] was completed by the end of the month, and the appearance of quotes from Hutchinson reflect the influence of Yale on Lindeman's ideas. He immediately set about catching up on correspondence and wrote the following letter to William S. Cooper, a plant ecologist at Minnesota (*12*):

> Enclosed is another—and greatly modified—version of my essay on the trophic-dynamic viewpoint in ecology. Dr. Hutchinson, needless to say, was immediately much interested in the ideas, contributed some of his own, and generously spent a lot of time with me in rounding them out. The Cedar Bog Lake data adapted themselves beautifully for illustrating the trophic principles. The greatest gaps seem to be in obtaining adequate terrestrial data.
>
> Dr. Hutchinson very strongly urged that the essay be published as soon as possible and has sent it off to Park for *Ecology* [see (*13*)]. I'm afraid you're going to say that I've hazarded a great deal of theory on very little information, and you may be right. I have a feeling, though, that at least some of the ideas are piquing enough to start some people making ecological studies on the basis of productivity and efficiency, and that would be quite gratifying even though some of the hesitantly proposed "principles" turn out to be wrong.
>
> I should like very much to have you and Dr. Lawrence comment on this latest brain-child, if you care to—even though it be a none-too-gentle reprimand. I'm really very grateful for all the criticisms and encouragement you've already given—and feel that many of the good parts of the paper (if any) were due to the stimuli given by yourselves and the spirited seminar discussions out at your home last year.
>
> Hoping that you have enjoyed a fruitful summer, are in excellent health and not too much pursued by hare-brained graduate students,
>
> I am, Ray Lindeman

Lindeman now devoted further work to the analysis of microfossils and the revisions of manuscripts in the senescent lake series (*14*).

The Rejection

In the middle of November, more than a month after he submitted the trophic-dynamic paper to *Ecology*, Lindeman received the letter of rejection. Park wrote, "[It is] with some reluctance and distress that I feel forced to take this action . . . [I] found your paper stimulating . . . [but] I am not really competent in this field." Both referees had recommended rejection because the paper was without sufficient evidence and premature, and therefore not suitable for *Ecology* (*15*). Lindeman was very distressed and wrote that he had great respect for the viewpoint of the referees but felt that they were intolerant of opinions other than their own. The paper presented "practical working methods for evaluating and integrating the complex processes acting within many types of natural communities—methods whose value could be tested by certain minor modifications of research programs. Because this approach has given reasonably satisfactory results in preliminary application, I feel that other ecologists (not necessarily limnologists) should be given an opportunity to consider this viewpoint with respect to their own problems" (*16*). He made plans to rework the manuscript and submit it to the *Quarterly Review of Biology*.

The referees of the paper were Chancey Juday at Wisconsin and Paul Welch at Michigan, the two most prominent limnologists in the country. In addition to specific minor criticisms of the data, the referees had the following general comments to make:

> JUDAY: A large percentage of the following discussion and argument is based on "belief, probability, possibility, assumption and imaginary lakes" rather than on *actual* observation and data. The chances are that the author's beliefs and imaginary lakes would be very different entities if he had a background of observations on fifty or a hundred of the 10000 lakes claimed by the state of Minnesota instead of on only one, and that a special type. According to our experiences, lakes are "rank individualists" and are *very stubborn* about fitting into mathematical formulae and artificial schemes proposed by man. . . . Some of the "broad generalizations" mentioned in the paper are certainly very broad; so broad in fact that they cannot be regarded as having much value.
>
> WELCH: I would raise the question of suitability for publication in *Ecology*. This paper is admitted by the author to be an essay, and while I do not wish to put myself in the position of suggesting to you what your editorial policy should be, I would express my own feeling that papers in the form of general essays should ordinarily be excluded. It seems to me unfortunate if the space which should be occupied by research papers is partly consumed by "desk produced" papers unless they be of a most unusual and significant kind. In my humble opinion this kind of treatment is premature. Limnology is not yet ready for generalizations of this kind. The basic background data for such a paper is far too fragmentary. If Dr. Lindeman could put this paper aside for ten years, then bring it out and see how it looks in the light of what we hope will be the added accumulation of limnological information, he might possibly congratulate himself that he deferred its publication. What limnology needs now most of all is research of the type which yields actual significant data rather than postulations and theoretical treatments.

The Acceptance

The lines of difference on the issue of publication were clearly drawn 4 days later when Hutchinson, writing to Park on general editorial matters for *Ecology*, enlarged specifically on the Lindeman manuscript (*17*):

> I also received your letter about Lindeman's work in which you courteously ask for my reactions as to the opinions submitted by the referees. I entirely understand your not wishing to publish the work, in the face of such adverse comments. In view of the fact that Dr. Lindeman himself felt uncertain as to its appearance, in spite of my favorable view, he submitted the manuscript to two plant ecologists with whom he has studied, both of whom happen to be on our editorial board, and who reported respectively that the work "looks excellent" and is "definitely in good shape for publication." May I suggest that you communicate to the referees (I think that internal stylistic peculiarities reveal their identity as men for whom I have great personal regard and who have been most kind to me on many occasions) this letter, *except for the preceding sentence*, that they may realize that most of the specific points challenged are matters for which I, rather than Lindeman, am respon-

sible. I am most anxious that the encouragement I gave him, to forward this paper for publication, shall not prejudice his reputation as an ecologist. My own view is that, if the work is published, after the ten years or so suggested by Referee 2 have elapsed, Lindeman will feel that he has played a very considerable part in a healthy reorientation of ecological research. Before that time, however, he will need a position somewhere and although I still think it most desirable to publish the work, I do not want my backing of it to be a handicap to him.

As regards the detailed comments of referee 1: . . .

. . . The second part of criticism 3 of Referee 1 and the comments of Referee 2 virtually reduce to a discussion of a) whether theoretical work is legitimate in ecology, and b) whether *Ecology* should print it.

My own feelings, quite apart from Lindeman's paper, are that such a theoretical study is very desirable and that *Ecology* should cover the whole field of the subject. I was very pleased to see that you printed Haskell's work, although I disagree with about one half of it, and sincerely hope that further contributions from that most stimulating individual will appear. Far from agreeing with Referee 2 as to what limnology needs, I feel that a number of far-reaching hypotheses that can be tested by actual data and which, if confirmed, would become significant generalizations, are far more valuable than an unending number of marks on paper indicating that a quantity of rather unrelated observations has been made. As an example, one of the things that has impressed me most in my study of Linsley Pond is the fact that the morphometry of the basin affects the vertical distribution of certain substances when the lake is stratified. The conditions for this to be apparent are clearly very special, though the underlying cause is probably of very general significance. Yet because no one has been sufficiently aware of the theoretical aspects of heating and transport of chemical material in stratified lakes, no cases have ever been published in which analyses were made at close enough vertical and temporal intervals to permit any judgment as to whether the phenomenon occurs in other lakes in North America. At times I have felt quite desperate about the number of opportunities that have been missed in the middle western regions for obtaining data confirming or disproving the hypotheses that have been forced on us by our little lake here. In genetics, experimental embryology, biodemography, and other sciences where the phenomena are not spread out over great ranges of time and space, it is possible for one worker to produce hypothesis after hypothesis, discarding those that are invalid after a few weeks' work in the laboratory. In field ecology, it is necessary to have data collected over many months or years, and for comparative purposes studies are needed on localities very widely separated in space. To obtain the kind of data required takes two or three years' work on a single locality; to suggest that any one individual should wait until he has completed investigations on fifty or one hundred lakes is ironical rather than practical. It is therefore most important that all ecologists should have the opportunity to acquaint themselves with the theoretical possibilities that may guide them in their collection of data, and that they should consider it their duty to acquire an objective understanding of the significance of any potentially fruitful hypotheses that may be advanced. This is, of course, the normal procedure in astrophysics, an even more expensive and time consuming science.

Because I feel that Lindeman's paper will actively encourage certain important kinds of investigation, I believe it should be published as soon as possible. The very fact that he has had to use fragmentary data indicates that without an orienting hypothesis, the need for obtaining the required observational and experimental results has not been clearly envisioned. As I have indicated, it is quite beyond the powers of one man to perform the investigation himself. Even should none of his generalizations ultimately hold, the work of disproving them will provide important information that would probably be obtained in no other way, and all authors should be allowed to take comfort in the words of Sir Thomas Browne, "the certainty here-of let the arithmetick of the last day determine . . . although at last we misse the truth, we die notwithstanding in harmless and inoffensive errors, because we adhere unto that, whereunto the examen of our reasons, and honest enquiries induce us" (*Pseudodoxia epidemica*, Bk. 6, Chp. VI).

You will realize that much of the material at the end of Lindeman's paper had occurred to me independently. As the biogeochemical treatise in which it is discussed progresses so slowly and threatens to assume such monumental proportions, it seemed best to hand him the relevant material, to use as he saw fit. This fact may in part explain my strong feelings on the matter, but over and above such feelings I hope I have made clear that an important question of policy seems to me to be involved.

Park sent a copy of Hutchinson's comments to the two reviewers, who still adhered to their earlier criticisms, and then wrote Lindeman, "if you care to revise your manuscript in any way you see fit and resubmit it to me, I shall try to find an impartial referee who will . . . make the final decision" (*18*). Ray agreed to resubmit the paper after Christmas, with several revisions incorporating suggestions of a number of ecologists to whom he had sent the work (*19*).

As Christmas approached Eleanor wrote to Ruth Patrick concerning a visit to the Philadelphia Academy of Natural Science over the holidays to identify diatoms (*20*), and Ray made plans to travel to Dallas to attend the meetings of the American Association for the Advancement of Science. He would deliver an address at these meetings coauthored with Hutchinson (*21*) in which many of the conceptual innovations of the trophic-dynamic paper were presented. He was also very busy producing the draft of manuscript 4 which he planned to send to Park.

It was shortly after returning from Dallas that Ray underwent a "mild recurrence of the jaundice attack I had in 1937" which put him in the Yale–New Haven Hospital for 3 weeks (*22*). In the middle of February he returned home but all field and laboratory work was suspended. On 13 January he had sent a copy of the revised trophic-dynamic paper to Victor Shelford, a well-known animal ecologist, and he was waiting for his response before submitting it again to *Ecology*. Shelford's letter came on 3 March (*23*):

> The paper seems to me to be very well written and on a very interesting topic. I have, however, not specialized in lake metabolism and so am not able to offer suggestions in that field, and wish you luck in going forward with the idea.

Within a week Ray had a new copy typed and sent to Park. He in turn sought an impartial third referee in the person of his colleague at Chicago, W. C. Allee, who was unenthusiastically neutral on the manuscript (*24*). The controversy surrounding the issue had become well known among a number of ecologists, and Allee's lack of strong support put the young editor of *Ecology* in a delicate position. On 23 March 1942, Park wrote to Lindeman (*25*):

> I have carefully considered your revised manuscript and am herewith accepting it for *Ecology*. I rather imagine that the original referees will still object to certain of its basic premises but I think it best to publish your paper regardless. Time is a great sifter in these matters and it alone will judge the question.

The Significance for Ecology

It seems appropriate to note several points of significance in the publication of Lindeman's paper. First, ecology at this time represented the merger of a number of rather independent lines of research; it was primarily derived from a very empirical tradition of field investigations somewhat systematic in nature and 19th-century natural history in which most generalizations were the inductive descriptions of data. There was immense interest in problems concerning the classification of observed ecological patterns, leading to a prolific terminology and the consequent conflicts of opinion concerning nomenclature (*26*). During his last year at Minnesota, for instance, Lindeman would gather with other graduate students in the home of William Cooper to debate the meaning of the many ecological terms and concepts found in *An Ecological Glossary* (*27*). This concern with the establishment of an appropriate language of ecology was probably the inevitable result of the independent development of plant and animal ecology, as well as limnology and environmental physiology. In its enthusiasm to solidify the classification of eco-

logical patterns into a nomenclatural description, the synthetic impulse in ecologists could easily lose sight of the underlying processes determining those patterns. Thus the first important consequence of Lindeman's paper was to stress the major role of trophic function, particularly quantitative relations, in the determination of community patterns through succession.

Second, Lindeman's paper established the validity of a theoretical orientation in ecology. Although the foundations of future ecological theory were being quietly established in the 1920's and 1930's (*28*), much of this work was considered of little relevance to the "real world"; and some 20 years would pass before its influence was felt (*29*). Up to this time the major tradition in ecological studies in the United States was the description and classification of plant and animal communities. Little truly theoretical work, involving the construction of mathematical models, had been published and incorporated into the body of accepted ecological knowledge. This can be clearly seen in the book *Bio-Ecology* which was published in 1939 and represented the summation of all previous ecological principles by the most eminent plant and animal ecologists of the time, Frederick Clements and Victor Shelford. The classificatory approach to the description of communities utilized the biome ("the great landscape types of vegetation with their accompanying animals") as its fundamental unit, and the earlier developmental stages of such units represented the process of community succession. Underlying this whole ecological approach was the metaphor of the developing organism, and the stable climax community is explicitly considered "a complex organism, or superorganism, with characteristic development and structure. As such a social organism, it was considered to possess characteristics, powers, and potentialities not belonging to any of its constituents or parts . . . the community, as noted above, is more than the sum of its individual parts, that it is indeed an organism of a new order" (*30*). By creating a theoretical model of trophic interactions, quantitatively represented by mathematical relations, Lindeman was able to develop a number of predictions with which the validity of the model could be assessed.

Third, the trophic-dynamic approach identified a fundamental dynamic process, energy flow, with which the seasonal trophic relations of organisms could be integrated into the long-term process of community change. Guided by the analogy between developing organisms and the dynamics of succession, most plant ecologists determined the correct classification of communities by changes in the abundance and distribution of species assumed to be characteristic of particular developmental stages. Limnology, more than ecology in general, had stressed the importance of productivity in order that various types of lakes might be set into a general classification based in large part on the abundance (biomass) of plankton and bottom faunal communities. This approach, however, failed to consider the metabolic relations of these "superorganisms" (*31*); and by introducing energetics, Lindeman reduced the processes of the food cycle to their most basic component. The importance of this innovation was even acknowledged by Paul Welch, one of the original referees of the paper. In the second edition of his book *Limnology*, first published in 1935, Welch added, in the chapter on biological productivity, a special section on trophic relations (*32*):

> Somewhat recently, certain investigators, notably Lindeman (1942), have attempted to analyze the events within a food complex in terms of energy. Because of the great paucity of detailed information basic to dependable formulation of such concepts, any discussion at present is largely hypothetical and must be regarded as suggestive only. Hints that these complex interrelations may eventually yield to mathematical analyses appear in the work of Lindeman and others. Entry into the speculative aspects of this subject will not be undertaken here. However, out of the pioneering work done thus far, there have arisen biological conclusions which seem to have certain validity.

Welch then continues to report the general conclusions of the trophic-dynamic paper, a result that surely would have pleased Lindeman.

Finally, the critical role of Hutchinson in the development and publication of this paper must be mentioned (*4*). Much of modern ecology has grown from the communal relations he was able to establish with those fortunate enough to work with him, and from the depth and endurance of his intellectual vision.

Illness and Death

As the spring of 1942 developed, Lindeman's health was not improving; and, in a letter to Don Lawrence in April, he wrote, "I am desperately anxious to get back to my own work, on which almost nothing has been done since Christmas, and hope to spend at least a few hours a day on it soon. The trouble is obscure—hepatic cirrhosis of unknown etiology, with a possibility that it may become progressively worse in spite of everything" (*33*). Lindeman had another hepatic attack at the end of April and soon wrote his close friend, Charles Reif, "We hope to be at the University of Pennsylvania next year, as I have a fellowship there, but (confidentially) there is a better than even chance I won't survive the summer. My liver trouble has gotten irregularly worse, in spite of the best doctors, and after 4 months is beginning to show visceral oedema. I expect to have an *exploratory* operation soon in the more or less desperate hope that they can find out what the *cause* is and then try for a cure. Eleanor is working at the Yale Library and should be able to continue if worse follows worse" (*34*).

On 15 June, Ray underwent surgery and died within 2 weeks. In an addendum to the trophic-dynamic paper, Hutchinson wrote (*35*):

> While this, his sixth completed paper, was in the press, Raymond Lindeman died after a long illness on 29 June 1942, in his twenty-seventh year. While his loss is grievous to all who know him, it is more fitting here to dwell on the achievements of his brief working life. The present paper represents a synthesis of Lindeman's work on the modern ecology and past history of a small senescent lake in Minnesota. In studying this locality he came to realize, as others before him had done, that the most profitable method of analysis lay in reduction of all the interrelated biological events to energetic terms. The attempt to do this led him far beyond the immediate problem in hand, and in stating his conclusions he felt that he was providing a program for further studies. Knowing that one man's life at best is too short for intensive studies of more than a few localities, and before the manuscript was completed, that he might never return again to the field, he wanted others to think in the same terms as he had found so stimulating, and for them to collect material that would confirm, extend, or correct his theoretical conclusions. The present contribution does far more than this, as here for the first time, we have the interrelated dynamics of a biocoenosis presented in a form that is amenable to a productive abstract analysis. The question, for instance, arises, "What determines the length of a food chain?"; the answer given is admittedly imperfect, but it is far more important to have seen that there is a real problem of this kind to be solved. That the final statement of the structure of a biocoenosis consists of pairs of numbers, one an integer determining the level, one a fraction determining the efficiency, may even give some hint of an undiscovered type of mathematical treatment of biological communities. Though Lindeman's work on the ecology and history of Cedar Bog Lake is of more than local interest, and will, it is hoped, appear of even greater significance when the notes made in the last few months of his life can be coordinated and published, it is to the present paper that we must turn as the major contribution of one of the most creative and generous minds yet to devote itself to ecological science.

References and Notes

1. R. L. Lindeman, "Ecological dynamics in a senescent lake," thesis, University of Minnesota, (1941). A copy of this work may be found in Kline Science Library, Yale University, New Haven.
2. R. Lindeman, *Ecology* **23**, 399 (1942).
3. Indications of the importance of this paper for the understanding of the functioning of ecosystems can be found in, "Dynamics of production in aquatic communities," *Ecol. Monogr.* **16**, 311 (1946); L. B. Slobodkin, "Energy in animal ecology," *Adv. Ecol. Res.* **1**, 69 (1962): V. F. Gallucci, "On the principles of thermodynamics in ecology," *Annu. Rev. Ecol. Syst.* **4**, 329 (1973); R. E. Ricklefs, "Energy flow in ecosystems," in *Ecology* (Chiron Press, Newton, Mass., 1973), chap. 41; R. B. Williams, "Computer simulation of energy flow in Cedar Bog Lake, Minnesota, based on the classical studies of Lindeman," in *Systems Analysis and Simulation in Ecology*, B. C. Patten, Ed. (Academic Press, New York, 1971), p. 543; see also, L. B. Slobodkin, "On the inconstancy of ecological theories," in *Growth by Intussusception, Ecological Essays in Honor of G. Evelyn Hutchinson*, E. S. Deevey, Ed. [published in *Trans. Conn. Acad. Arts Sci.* **44**, 291 (1972)] for a revisionary assessment of Slobodkin's own work. For a historical treatment and updating of the limnological studies, see the appropriate regional chapters in *Limnology in North America*, D. Fry, Ed. (Univ. of Wisconsin Press, Madison, 1963).
4. For more details, see R. E. Cook, in preparation. Most of the information in this article has been drawn from the papers of R. Lindeman deposited in the Archives of Sterling Library, Yale University.

4a. E. P. Odum, *Science* **195**, 1289 (1977).

5. R. L. Lindeman, "The developmental history of Cedar Creek Bog, Minnesota," in *Am. Midl. Nat.* **25**, 101 (1941). This paper is the first in a series of works entitled "Ecological studies of a senescent lake" of which five were finally published. This was not Lindeman's first publication which was "Some affinities and varieties of the planktonic rotifer, *Brachionus havanaensis* Rousselet," *Trans. Am. Microsc. Soc.* **58**, 210 (1939). Other papers in the "senescent lake" series are: II. M. F. Buell and H. F. Buell, 1941. "Surface level fluctuations in Cedar Creek Bog, Minnesota," *Ecology* **22**, 317 (1941); III. R. L. Lindeman, "Seasonal food cycle dynamics in a senescent lake," *Am. Midl. Nat.* **26**, 636 (1942); IV. "Experimental simulation of winter anaerobiosis in a lake," *Ecology* **23**, 1 (1942); V. R. L. Lindeman, "Seasonal distribution of midge larvae in a senescent lake," *Am. Midl. Nat.* **27**, 428 (1942). These papers, along with the trophic-dynamic paper, comprise the published works of Lindeman. For a recent addition appropriately considered in this series, see M. F. Buell, H. F. Buell, W. A. Reiners, "Radial mat growth on Cedar Creek Bog, Minnesota," *Ecology* **49**, 1198 (1968).
6. R. L. Lindeman, "Seasonal food cycle dynamics in a senescent lake," *Am. Midl. Nat.* **26**, 636 (1942).
7. All correspondence, and draft manuscripts cited in subsequent footnotes, may be found in box 1, Lindeman Papers, in the Archives of Yale University. Four draft manuscripts exist in the Archives: manuscript 1 (February 1941); manuscript 2 (March 1941); manuscript 3 (September 1941), which is shortly after Lindeman arrived at Yale; and manuscript 4 (January 1942) which was written after the rejection of manuscript 3.
8. Owing to a childhood accident, Ray was partially blind in one eye. This made him somewhat dependent upon Eleanor for microscopic identification of specimens. She was a trained biologist herself, having graduated from the University of Minnesota in 1939; and in the last year they spent together, she examined diatoms in sediment cores taken from Cedar Creek Bog. This resulted in an unpublished manuscript coauthored with Ray, "Microfossils in the sediments of a senescent lake, and their successional significance: a preliminary report." Mrs. Eleanor Burns has been of considerable help in my research.
9. E. S. Deevey had completed his thesis work on "Typological succession in Connecticut lakes" at Yale and had taken a teaching job at Rice University in 1939.
10. University of Wisconsin, *A Symposium on Hydrobiology* (Univ. of Wisconsin Press, Madison, 1941).
11. Lindeman refers to this work as "Recent advances in limnology (in manuscript) 1942." The manuscript was distributed by the Osborn Zoological Laboratory, Yale University, and copies exist in Kline Science Library and Yale Archives in the Hutchinson papers.
12. R. L. Lindeman, letter dated 29 September 1941. Although at the University of Minnesota Lindeman was officially the student of Samuel Eddy, a fish systematist and limnologist, it appears that he was more strongly influenced by William S. Cooper, a plant ecologist in the botany department who was the intellectual stimulus for informal meetings of graduate students and younger faculty to discuss ecological concepts and definitions.
13. Hutchinson was a consulting editor of *Ecology* at this time and Thomas Park at the University of Chicago was zoological editor.
14. The seasonal food cycle paper was originally submitted to *American Midland Naturalist* on 3 May 1941. In rewriting the trophic-dynamic paper (manuscript 3), Lindeman extracted part of the comparative discussion of productivity from the seasonal food cycle paper and incorporated it into manuscript 3 to provide supporting evidence for some of the theoretical concepts. On 29 September he wrote a letter to the editor of *American Midland Naturalist* requesting changes in the seasonal food cycle paper; and, full of confidence, he wrote in the revised productivity section of this work, "The theoretical aspects of apparent and true food-group efficiencies for Cedar Bog Lake is discussed in detail in a forthcoming paper (Lindeman, 1942 c)." He was later (17 November 1941) to strike this reference with the comment, "I have just decided that this theoretical paper is too premature and should not yet be published for some time."
15. Park to Lindeman, 14 November 1941.
16. Lindeman to Park, 18 November 1941.
17. Hutchinson to Park, 18 November 1941.
18. Park to Lindeman, 8 December 1941.
19. Lindeman to Park, 13 December 1941. Most of these suggestions involved relatively minor revisions (except for his concept of climax equilibrium) and were principally contributed by J. R. Carpenter, W. S. Cooper, E. S. Deevey, A. Hodgeson, D. B. Lawrence, H. J. Lutz, A. E. Parr, and V. E. Shelford.
20. Eleanor Lindeman to Ruth Patrick, 11 November 1941.
21. G. E. Hutchinson and R. L. Lindeman, "Biological efficiency in succession" *Bull. Ecol. Soc. Am.* **22**, 44 (1941).
22. Lindeman to Eddy, 10 February 1942.
23. Shelford to Lindeman, 11 March 1942
24. T. Park, personal communication.
25. Park to Lindeman, 23 March 1942. Park was clearly a strong supporter of a more theoretical approach to ecology [see, for instance, W. C. Allee and T. Park, "Concerning ecological principles," *Science* **89**, 166 (1939); and T. Park, "The laboratory population as a test of a comprehensive ecological system," *Q. Rev. Biol.* **16**, 274 and 440 (1941)] and he played an important role in bringing theoretical and laboratory population studies into the main body of ecological work.
26. This was a problem of considerable concern to many ecologists of the day. See, for example, book reviews by C. Elton entitled "American ecology" and "Scholasticism in ecology," in *J. Anim. Ecol.* **9**, 148 and 151 (1940).
27. J. R. Carpenter, *An Ecological Glossary* (Univ. of Oklahoma Press, Norman, 1938).
28. A. J. Lotka, *Elements of Physical Biology* (Williams & Wilkins, Baltimore, 1925); G. F. Gause, *The Struggle for Existence* (Williams & Wilkins, Baltimore, 1934); V. Volterra, "Variazioni e fluttuazioni del numero d'individui in specie animali convivanti," *Mem. Accad. Lincei* **2** (No. 6), 31 (1926).
29. L. B. Slobodkin, *Growth the Regulation of Animal Populations* (Holt, Rinehart and Winston, New York, 1961).
30. F. E. Clements and V. E. Shelford, *Bio-Ecology* (Wiley, New York, 1939), pp. 20–21. It should be noted that this organismic approach paralleled the whole conceptual framework being established in developmental biology at this time; see D. H. Harroway, *Crystals, Fabrics and Fields* (Yale Univ. Press, New Haven, 1975).
31. G. E. Hutchinson, "Review of *Bio-Ecology*," *Ecology* **21**, 267 (1941).
32. P. Welch, *Limnology* (McGraw-Hill, New York, ed. 2, 1952), p. 350.
33. Lindeman to Lawrence, 13 April 1942.
34. Lindeman to Reif, 16 May 1942.
35. Addendum, G. E. Hutchinson, *Ecology* **32**, 417 (1942).

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