

lism formed the intellectual core of what later became ecosystem ecology.

4 The Metabolic Imperative

From the viewpoint of a cat, mice are machines for converting plants into food.

—LAWRENCE B. SLOBODKIN, *Growth and Regulation of Animal Populations*



IN A REVIEW OF ONE of Frederic Clements's last major works, the Yale limnologist G. Evelyn Hutchinson remarked that if a community were an organism then it ought to have a form of metabolism.¹ This suggestive idea was never explored by Clements, and Hutchinson complained that Clementsian ecology had progressed little beyond the description and classification of communities. The criticism was not entirely fair. Whatever its shortcomings, Clementsian theory was oriented more toward process than classification.² Yet in his later years the great plant ecologist had done little to expand his organismal analogies, and to Hutchinson's aggressive intellect Clements's ideas appeared a bit shopworn.

By 1940, when Hutchinson's review was written, the contours of ecology were beginning to change. Like most of his contemporaries, Hutchinson refused to consider the community an organism. Yet the idea that the movement of energy and materials through the community was analogous to the metabolism of an organism intrigued him. Indeed, together with his close contemporary, Charles Elton, Hutchinson did much to place the study of this "community metabolism" at the heart of post-World War II ecology. In this chapter I consider the development of this physiological analogy and its theoretical ramifications at the hands of Elton and Hutchinson. Combined with the Clementsian notion of community development, community metabo-

Charles Elton and Trophic Dynamics

Superficially, Charles Elton (figure 3) seems an unlikely historical candidate for stimulating the development of ecosystem ecology. In later life he showed little enthusiasm for either the new specialty or its emphasis on energy. Ecology, so he claimed, was "scientific natural history."³ Elton delighted in detailed, descriptive field studies, and he found his inspiration in the Darwinian tradition of natural history rather than in the laboratory sciences. Nonetheless, through his insistence on the importance of feeding or trophic relationships, Elton laid the intellectual foundation for the study of energy flow in ecosystems.

Reminiscing on his childhood, Elton acknowledged an early interest in observing and collecting animals, an interest further stimulated by reading Darwin's *On the Origin of Species* when he was sixteen.⁴ The transition from neophyte collector to mature scientific naturalist occurred when he entered Oxford shortly after the end of World War I. There he studied zoology under Julian Huxley, who was gaining an international reputation for his work on avian behavior. Perhaps more significantly, Elton accompanied Huxley on the Oxford University Spitsbergen Expedition, the first of three such journeys to the arctic that Elton made prior to writing his first book on ecology. These trips introduced Elton to field research, and they did much to shape his views on the nature of biological communities.⁵

Most earlier work on communities had been done by botanists, and Elton was willing to accept ecological succession as an important unifying concept. His views on the matter reflected the modified Clementsian scheme taught at Oxford by Arthur Tansley during the late 1920s. But community development was an inherently unattractive area of research for the zoologist. Unlike the botanist who could more easily study the slow changes in firmly rooted plant communities, the zoologist was forced to contend with constantly moving populations of often well-concealed animals. Zoologists, notably Victor Shelford, had completed some suggestive studies on succession in animal communities. In most cases, however, zoologists simply accepted the successional patterns previously determined for plant communities and then described the accompanying changes in the fauna. Elton had little enthusiasm for such derivative research.

In his audacious *Animal Ecology* (1927), no less remarkable because it was completed in three months when he was only twenty-six years old, Elton charted a new course for community ecology. "Animals are not always struggling for existence," Elton wrote, "but when they do begin, they spend the greater part of their lives eating. . . . Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food-supply."⁶ "Eating," a much more obvious phenomenon in animals than in plants, provided the zoologist with an important unifying concept. What unified animal communities—indeed, what made "community" a useful zoological concept—was the fact that within the community animals fed on other organisms. Whether one considered the microorganisms in a mouse's gut, the inhabitants of a small pond, or the fauna of an equatorial rain forest, the general pattern of feeding relationships was identical.⁷

The "general ground plan" of every animal community was an organized system of herbivores, carnivores, and scavengers.⁸ But these traditional biological terms were too crude for the trophic analysis that Elton was creating. Through the course of evolution most animals had become specialists: an animal was not simply a carnivore; more likely it was a carnivore with rather restricted food requirements. Typically each species had an optimal food size. Potential prey that were too large could not be caught and destroyed; prey that were too small would not supply the nutritional requirements of the predator. This optimal range of food—not too big but not too small—determined the animal's niche in the community.⁹ In describing the niche of an animal the ecologist was saying something about that species' status within the community, what the species was "doing" there. As Elton whimsically put it, "When an ecologist says 'there goes a badger' he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said 'there goes the vicar.'¹⁰ Whatever Elton's opinion of the role of the clergy in English society, the role of an animal was always to eat or be eaten: "the 'niche' of an animal means its place in the biotic environment, its relations to food and enemies."¹¹

Recent critics have complained that the concept of niche is vague, little more than post hoc descriptions of the characteristics of animals. Thus, niche has little predictive value.¹² But in *Animal Ecology*, Elton suggested that this concept could play an important predictive role in ecological research. Communities shared a common ground plan, and even very different communities contained parallel niches. Therefore, given an unknown community, the ecologist ought to be

able to predict the types of animals that existed there. Furthermore, it could be used as an important comparative tool for studying communities. Although taxonomically unrelated, species in two communities often played equivalent functional roles. For example, a common niche in the animal communities surrounding Oxford was that "filled by birds of prey which eat small mammals such as shrews and mice."¹³ This niche was occupied by tawny owls in oak forests and by kestrels in grasslands.

Because animals tended to be specialists, feeding relationships in communities followed definite patterns. One could conceive of a *food chain* linking several niches in the community. This idea was not completely novel in 1927. It was a common practice among zoologists and fishery biologists to diagram feeding relationships with arrows leading from prey to predator. What made Elton's concept of food chain unique was the way he generalized it. The food chain represented the fundamental organizational structure or ground plan shared by all communities. And the passage of food through the chain of niches constituted the fundamental process that held communities together.

The "basic class" in the animal community was the herbivores, which converted plant material into animal tissue. A particular species of herbivore was consumed by certain carnivores, which in turn were eaten by other carnivores. The limits of such a food chain were set by the relative size and numbers of animals occupying each niche. Herbivores tended to be more abundant than the carnivores that ate them; the carnivores were living off the excess "margin" of the herbivore class. Carnivores that ate other carnivores tended to be both larger and fewer than their prey. In other words, as one moved up the food chain each level provided a smaller margin of food to the next. Thus at some point, the food chain reached its limit when the available food was too small to support an additional class of carnivores. This important relationship between predator and prey, which limited the length of food chains, Elton termed the *pyramid of numbers*.

In reality, this simple feeding scheme, represented by food chain diagrams and the pyramid of numbers, was complicated by several factors. Animals, in fact, had two sets of enemies: large carnivorous predators and small parasites. Field mice provided food for not only owls and kestrels but also fleas. Fleas were parasitized, in turn, by protozoans and bacteria. Thus, each level in a typical food chain was also the starting point for shorter, parasitic food chains. Other animals in the community lived by scavenging dead organic material, and a complete picture of feeding relations also required these scavenger or decomposer food chains. Finally, numerous food chains

were linked together to form what Elton referred to as a *food cycle* and what a later generation of ecologists called a *food web*. Some animals—for example, copepods in a pond—were so numerous that they could support several different species of carnivores. Copepods were the “key industry” on which the entire economy of the community depended; many food chains radiated from this common supplier of food.

Though greatly simplified, Elton’s idealized food cycle explained both the stability and the periodic disturbances found in nature. All populations had the potential for exponential increase. Left unchecked, this exponential increase would destroy the delicate balance that existed within communities. This occasionally happened, but usually populations remained relatively stable. Every animal population, Elton argued, had an optimum density. Because the environment was always fluctuating, the number of animals never remained constant, but populations tended to track a shifting optimum set by available food. Although food supply set the ultimate limitation on population growth, starvation was rarely the primary mechanism for controlling growth. In most cases, numbers began to decrease before the population faced starvation. The food cycle acted as a mechanism for this regulation. As the number of individuals increased, that population tended to become a more conspicuous target for predators. As numbers declined, predators shifted their eating habits and concentrated on another more plentiful prey species. Thus prey species were dependent upon predators for their own well-being; the predators acted as a kind of regulator maintaining the optimal numbers of their prey. Forty years earlier, Stephen Forbes had spoken of a “community of interest” between predator and prey; Elton shared this view. Speaking of the relationship between deer and their carnivorous “enemies,” Elton noted that the predators “are in fact only hostile in a certain sense, in so far as they are enemies to individual deer; for the deer as a whole depend on them [predators] to preserve their optimum numbers and to prevent them [deer] from over-eating their food-supply.”¹⁴

Elton presented the food cycle as a regulatory mechanism for maintaining equilibrium within the community. But important as it was, the food cycle was an imperfect regulator. Small herbivores sometimes reproduced so rapidly that predators could not control their numbers. For example, populations of lemmings, voles, and other microtine rodents periodically exploded. Migration served as one kind of safety valve for the community; as rodent populations reached high densities individuals dispersed to less populated areas. Another

more important control mechanism was epidemic disease. The population cycles that so interested Elton were largely the result of periodic, unrestrained growth followed by catastrophic death, often the result of epidemic disease.¹⁵ The food cycle, disease, migration, and other regulatory mechanisms maintained stability in the animal community, but this stability was a fragile equilibrium often subject to disruption.

Animal Communities and the Economy of Nature

Elton was a careful observer of nature who in later life spent twenty years completing an exhaustive study of animal communities near his home in Oxford.¹⁶ He consistently emphasized the importance of such detailed field research as a foundation for ecology. But Elton was no naive empiricist. The growth of a coherent science depended heavily upon bold, general theories. Such theories, Elton claimed, were like carnivorous animals or powerful enzymes, capable of attacking and digesting apparently unrelated pieces of data.¹⁷ The real genius of the young Elton, so obvious in *Animal Ecology*, was his ability to cut through the complexity of nature to uncover a more fundamental simplicity. Relying on a relatively small body of empirical evidence, Elton forged a set of basic ecological principles. These principles served as not only explanations but also guides for future empirical studies:

The food-relations of animals are extremely complicated and form a very closely and intricately woven fabric—so elaborate that it is usually quite impossible to predict the precise effects of twitching one thread in the fabric. Simple treatment of the subject makes it possible to obtain a glimpse of the principles which underlie the superficial complication, although it must be clearly recognized that we know at present remarkably little about the whole matter.¹⁸

This sophisticated view of idealization provided a powerful rationale for studying ecology. Because, for all intents and purposes, every animal community shared a common economy or ground plan, the ecologist could investigate the simplest community and draw generalizations applicable to the most complex.¹⁹

Many of Elton’s most fertile ideas were derived from his studies of very simple arctic communities. For example, his concept of the food cycle developed out of an early biological survey of a small arctic

island.²⁰ In contrast to a complex woodland community in rural England, which might contain in excess of ten thousand species of animals, the impoverished fauna of Bear Island was represented by less than one hundred.²¹ Elton's diagram of the food cycle of Bear Island (figure 4) included perhaps thirty-five animals, although terms such as "Diptera," "Protozoa," and "Marine Animals" obviously referred to more than one species. This elegant picture of the feeding relations on Bear Island did not emerge from years of detailed empirical study; he and his coworkers completed his survey of the animals inhabiting the island during a ten-day excursion when Elton was still an undergraduate in his early twenties. Truly remarkable was that the precocious biologist, using this brief investigation and a handful of other studies, arrived at fundamental principles of trophic dynamics—and that, at twenty-six years of age, he was able to convince other ecologists that they were valid.

A central theme running through *Animal Ecology* is the belief that communities are highly integrated, self-regulating entities. In discussing self-regulation Elton employed both organismal and mechanical metaphors, but the most striking analogy that Elton developed was one between animal communities and advanced industrial societies:

Throughout this book I have used analogies between human and animal communities. These are simply intended as analogies and nothing more, but may also help to drive home the fact that animal interrelations, which after all form the more purely biological side of ecology, are very complicated, but at the same time subject to quite definite economic laws.²²

Elton's economy of nature was based upon a kind of supply and demand system. Plants, which Elton barely considered, formed the raw materials for the herbivorous "key industries" of the community. The numbers of carnivores at the higher levels of each food chain were ultimately determined by the productivity of these key industries. Despite the potential for exponential increase, populations tended to oscillate about an optimum density set by the food supply. "This optimum number is not always the same and it is not always achieved," Elton admitted, "but in a broad way there is a tendency for all animals to strike some kind of mean between being too scarce and too abundant."²³ Borrowing an illustration from the sociologist Alexander Carr-Saunders, Elton compared the conditions faced by animal populations with the problem faced by the employer desiring an optimum number of workers: too few workers meant less than maximum productivity, while too many workers meant a decrease in profit.²⁴

Nature's economy tended to be orderly and balanced, but like hu-

man industrial societies, animal communities were not completely free from violent and unpredictable events. An animal population occasionally increased beyond its optimal density, and this overpopulation could result in epidemic disease or starvation. The microtine population cycles that so interested him were obvious examples that Elton used to illustrate this phenomenon. But even more striking cases of catastrophic population fluctuations could be found in non-cyclic species. Among other examples, Elton pointed to the now classic story of the mule deer inhabiting the Kaibab Plateau of Northern Arizona.²⁵ Prior to 1906 the population of deer had been maintained at about 4,000 individuals by wolves, mountain lions, and other predators. Beginning in 1906 the federal government began an aggressive program of exterminating predators. By 1931 most of the deer's natural enemies had been trapped or shot: 781 mountain lions, 30 wolves, 4,889 coyotes, and 554 bobcats. Unrestrained by predation, the population of deer expanded to approximately 100,000, a number far in excess of what the habitat could support. Starvation resulted in the death by the thousands, and eventually the population dwindled to some 10,000 deer. This scientific account has been challenged,²⁶ but for Elton, writing in the 1920s, it illustrated two important ecological generalizations. In a dramatic way it demonstrated that animal populations were capable of not only violent fluctuations but also self-regulation of the animal community as a whole. Temporary changes in a single population might have far-reaching effects on the food cycle of the community, but generally a natural balance was eventually restored. "In fact," Elton concluded, "if several important key-industry species become suddenly very abundant or very scarce, the whole food-cycle may undergo considerable changes, if only temporarily. The various automatic balanced systems which exist will tend to bring the numbers, and therefore the food-habits, back in the long run to their original state."²⁷

The idea that nature formed a kind of well-regulated industrial economy was the dominant theme in Elton's early writings, but he was not entirely comfortable with this rather mechanistic picture of animal communities. In fact, there was a certain conflict in Elton's ecology between the industrial analogy and a conviction that nature was indeterminate, that stochastic processes were constantly interfering with the machinery of nature. So while he could write so eloquently of the "automatic balanced systems" that regulated communities, he could almost simultaneously reject the notion that there was a "balance of nature." In a series of lectures presented only two years after the publication of *Animal Ecology*, Elton stated that although the idea

of balance was popular among biologists, it was untrue. "The balance of nature' does not exist," Elton declared, "and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude."³⁸ Elton also questioned whether communities were machine-like:

The simile of the clockwork mechanism is only true if we imagine that a large proportion of the cog-wheels have their own main springs, which do not unwind at a constant speed. There is also the difficulty that each wheel retains the right to arise and migrate and settle down in another clock, only to set up further trouble in its new home. Sometimes, a large number of wheels would arise and roll off in company, with no apparent object except to escape as quickly as possible from the uncomfortable confusion in which they had been living.³⁹

This rather striking statement did not necessarily reflect an intellectual conversion after the publication of Elton's first book; indeed, one can find similar, though muted, allusions to the unpredictability of nature in *Animal Ecology*. Rather, the thematic differences in his two early books reflect a deep-seated intellectual tension that ran through Elton's ecology. The probable sources of this tension were diverse.

To a certain extent, Elton's problem appears inherent to ecology. The same intellectual dichotomy can be found in Darwin's discussion of the entangled bank, and it continues to be source of considerable controversy in ecology today.⁴⁰ Elton was simultaneously tackling problems in population dynamics and community metabolism. Several years later, G. Evelyn Hutchinson, who was also interested in both these areas of ecology, suggested that studying them required two quite different points of view.⁴¹ Population biologists tended to take a *merological* perspective, focusing upon independent individuals and assuming that populational phenomena determined higher level community properties. In contrast to this bottom-up approach, other ecologists, particularly those who later studied ecosystems, took a *holological* approach by studying the flow of materials and energy through food webs without considering the individuals that made up the web. Hutchinson, an eclectic biologist, seemed capable of making the transition from one perspective to the other effortlessly. Most other ecologists have not been so adept, for the change in perspective seems to entail more than simply differing points of view. Ecological terms and concepts also change meanings. For example, from the merological perspective, populations are not usually seen as parts of a community in the sense that gears are parts of a clock. Rather, they are "parts" only in the sense that together they form an aggregation. From such a

point of view a process such as competition is often viewed as no more than an interaction among independent individuals. From the holological perspective, however, the parts of a biological system are quite often visualized as pieces of a complex mechanical-organic entity. In such a context, competition may be viewed as a kind of cybernetic or quasi-physiological *function* that stabilizes the entire community. The conundrum posed by these two perspectives persists today, and it is perhaps not surprising that in his path-breaking early work, Elton was simultaneously attracted and repelled by the clock metaphor.⁴²

To explain Elton's contrary views on the balance of nature, one might also consider his use of analogy. He may have considered these merely illustrative figures of speech, but the particular analogies that he chose are revealing. To create a "scientific natural history" Elton needed to formulate fundamental laws and principles, and he looked to human sociology and economics for models. But writing during the uncertain 1920s, Elton could not be too sanguine about social and economic harmony, balance, or optimality. Such notions ran counter to the prevailing skepticism that characterized the work of many young intellectuals during the post-World War I years.⁴³ In 1926 one might be guardedly optimistic that industrial capitalism was basically sound, but it would have been difficult to be too confident about the future. Throughout the decade Britain's industrial machine had been "throttled down."⁴⁴ Chronic high unemployment, a trade imbalance, and labor unrest plagued the British economy. Elton's own professional situation, teaching part-time and working as a temporary consultant for the Hudson Bay Company, was particularly insecure. When the Great Depression began, Elton lost his job with the fur-trading company and scraped by on small research grants.⁴⁵ Perhaps not surprisingly, the industrial society that Elton saw in nature, though basically stable, was at times subjected to unpredictable and violent disturbances.

Elton's contrary views on the balance of nature also reflect quite different objectives in writing his two early books: *Animal Ecology* (1927) and *Animal Ecology and Evolution* (1930). In *Animal Ecology* he sought to lay out the fundamental principles of community ecology, and not surprisingly the major theme running through the discussion is the regularity of nature. He intended *Animal Ecology and Evolution*, a very different book, to critique widely accepted evolutionary ideas. Elton was highly critical of some Darwinians for believing that natural selection always produces adaptation. He accused them of accepting a naive evolutionary version of perfect adaptation, a "gossamer" of reassuring beliefs that every structure and behavior is of use in the

struggle for existence.³⁶ Elton seemed painfully aware that the themes developed earlier in his *Animal Ecology*—balance, optimality, and self-regulation—tended to support this adaptationist position. In *Animal Ecology and Evolution* he turned his back on these themes; in fact, he parodied them.³⁷ He emphasized, instead, the capricious side of nature; animals could never be perfectly adapted in a constantly changing world.

Elton's own evolutionary ideas were complex, and they provided yet another source of tension in his ecological writings. He considered himself an heir to the Darwinian tradition in natural history, and he believed that natural selection was an important evolutionary mechanism. Like many other ecologists of the period, Elton considered natural selection to be a general process operating at all levels of organization from cells to communities.³⁸ It also served as a "potent stimulus" for ecological research and a "coordinating principle" for organizing ecological data.³⁹ Without the digestive juice of natural selection, population studies produced only a mass of unassimilated data. Finally, natural selection was an important part of the "automatic balanced systems" that maintained communities in equilibrium. This commitment to natural selection notwithstanding, Elton recoiled from what he considered the deterministic implications of Darwinian theory. "The Darwinian theory," he wrote, "which I take to be mainly true as far as it goes, regards animals as stationary units, or at any rate units with regular ecological habits, and acted upon by a number of selective eliminating agents. Darwinism, in fact, implies the selection of helpless bundles of flesh by an environment which lacks any traces of biological purposiveness."⁴⁰

Given this attitude it is perhaps not surprising that Elton accepted genetic drift as an important mechanism for nonadaptive evolution.⁴¹ But his deep-seated philosophical commitment to free will also led him to accept less orthodox evolutionary explanations. He was convinced that animals have some control over their evolutionary destinies. Animals, Elton believed, possessed an innate "awareness of environmental harmony."⁴² This was more than a simple mechanical response to environmental stimulus; even insects were capable of making conscious choices. Through the gradual evolutionary emergence of mental activity, animals came to rely increasingly upon purposive behaviors. In higher animals, such purposive behaviors, or what Elton referred to as "traditions," might rival natural selection in evolutionary significance. "It is clear, then," Elton argued, "that among the higher animals we can perceive a method of evolution along a mental plane, unconnected with the spread of new mutations,

a method which leads on a small scale to the production of customs, cultures, and gregarious habits, similar to those found in man."⁴³

Elton apparently took his ideas on tradition—as well as some of his views on population dynamics—from Alexander Carr-Saunders. In his book *The Population Problem*, the British sociologist drew a distinction between animal evolution controlled by purely biological processes and human evolution guided, in part, by cultural traditions.⁴⁴ Elton blurred this distinction and argued that animals, too, have primitive traditions. Many behavioral traits, particularly in birds and mammals, were not inherited in a genetic sense; they resulted from parents teaching their offspring. For example, a mother bear swats her cub when it plays with something dangerous. Having no genetic basis, Elton argued, such maternal behavior could not arise through natural selection; it must have evolved through a rudimentary form of cultural transmission.

In the end, Elton presented his readers a rather eclectic picture of the animal world:

The real life of animals is therefore a compound of many things: fixed and predetermined limits impressed by the environment; the relations of the sexes; the survival of things that are useful; a certain free will in the matter of choosing between good and evil surroundings, accompanied by a great deal of movement; a fairly large amount of pure chance; and sometimes a growing stock of new ideas born out of contact with new situations—Predetermination, Sex, Materialism, Free Will, Destiny, Originality, and Tradition.⁴⁵

Predetermination and free will—Elton could hardly have it both ways. This apparent contradiction was symptomatic of the delicate and unstable equilibrium that existed in Elton's early writings. He was simultaneously attracted and repelled by a nature governed by mechanical law. Nature might be a highly mechanized, industrial society subject to deterministic natural laws, but at the same time it was a more chaotic world where even lowly creatures possessed considerable freedom to make choices.

Perhaps wisely, Elton never attempted to reconcile these views in a grand synthesis. After 1930, he directed his energies toward detailed surveys of local communities and studies of microtine population cycles. Late in his career he expressed a certain impatience with general theory.⁴⁶ But during that brief intellectual efflorescence of the late 1920s, Elton created an enormously flexible and fruitful theoretical scheme. The concept of community developed by Frederic Clements and other botanists had been plagued with an inherent rigidity;

community always referred to the plants inhabiting this or that particular geographical area. For Elton, the community became a much more abstract concept: it could refer equally to the intestinal fauna within a mouse or the inhabitants of the coniferous forest stretching across northern Canada; in either case, the same ecological principles applied. Animals formed a community precisely because they were organized into definite feeding patterns. The concepts of niche, food chain, food cycle (later referred to as food web), and pyramid of numbers became formative elements in the embryonic study of trophic dynamics, research that would become a major growth area in post-World War II ecology.

G. Evelyn Hutchinson: An Embryo Ecologist and an Embryonic Ecology

Elton's *Animal Ecology* was an extraordinarily successful book. After its initial appearance in 1927 it was reprinted eight times, and a paperback edition first released in 1966 went through another three printings within five years. Although it had originally been aimed at a general audience, Elton's first book had a profound impact upon professional ecology. According to the British ecologist Amyan MacFadyen, it "has probably inspired more ecological research than any other work."⁴⁷ One ecologist influenced by reading *Animal Ecology* when it first appeared was G. Evelyn Hutchinson (figure 5), then a young instructor at the University of Witwatersrand in South Africa. Later in his career, Hutchinson referred to the book as "deeply fundamental" and recalled that "it proved a stimulus by showing me that what I wanted to do in biology was indeed a significant part of the science."⁴⁸ For more than half a century Hutchinson pursued many problems posed by Elton's early book, but Hutchinson's approach to these problems was strikingly different from that of the author of *Animal Ecology*.

Elton's nonmathematical approach placed significant limitations on the development of ecological theory. He had made an important step by abstracting the concept of community from specific geographical instances; however, there was a tension between this process of abstraction and Elton's commitment to "scientific natural history." In contrast to the elegant picture of the animal community presented in his first book, what emerged from Elton's later research was detailed

description only loosely draped upon the earlier theoretical framework.

Hutchinson was not a pure theoretician. Like Elton, his research was a mixture of theoretical and empirical studies, including much work on the natural history of aquatic invertebrates. But Hutchinson was much more adept at the process of idealization. In contrast to Elton, whose nonmathematical ecology never strayed far from his descriptive natural history, Hutchinson was comfortable with the newer mathematical theory in ecology that began to develop during the late 1920s. Like the cyberneticians whom he admired, Hutchinson was quite willing, on occasion, to abandon Elton's natural history; for Hutchinson, nature was often cast as a "black box" whose inputs and outputs were the primary focus of study. This highly abstract approach to theory had a significant effect on the development of ecosystem ecology. Some factors that influenced Hutchinson's rather unique style of research can be gleaned from his biography.

Like Elton, who was two years his senior, Hutchinson grew up in an academic environment. Hutchinson's father, a chemist at Cambridge University, encouraged his son's boyhood interests in natural history and geology.⁴⁹ These informal scientific interests were reinforced when young Evelyn attended Gresham's School, one of the few English public schools to emphasize the sciences rather than the more traditional classical curriculum. Hutchinson always maintained an interest in the natural history of organisms. But unlike Elton, whose aversion to the physical sciences was undisguised, Hutchinson reserved central roles in his ecology for both chemistry and geology.

Charles Elton's ecological interests were set early in his undergraduate career at Oxford. In contrast, Hutchinson pursued a rather eclectic education at Cambridge. From boyhood he had become familiar with many scientists at the university. But apparently no one served the role of mentor in the way that Julian Huxley did for Elton. In his memoir, subtitled *Recollections of an Embryo Ecologist*, Hutchinson characterized his college experience as that of "a hunter and gatherer rather than that of someone settled in the industrious pursuit of intellectual agriculture."⁵⁰ This eclecticism became one hallmark of his career as a scientist.

After a year at the Stazione Zoologica in Naples and two years of teaching in South Africa, Hutchinson was appointed an instructor in the zoology department at Yale University in 1928. There a number of circumstances conspired to bring together the disparate strands of his early training, creating a unique approach to ecological research. These circumstances deserve extended consideration.

Biogeochemistry of a Connecticut Lake

Charles Elton had laid the theoretical groundwork for the development of trophic dynamics with his discussion of food chains, niches, ecological pyramids, and the food cycle. These concepts were fundamental to the study of a community metabolism, but in retrospect Elton had missed a crucial distinction between the flow of energy and the cycling of materials in ecological systems. In one of his earliest papers Elton discussed a "nitrogen cycle," a term he used interchangeably with food cycle. However, this nitrogen cycle is not the one familiar to the ecology student of today.³¹ Implicit in Elton's diagram is the idea that both matter and energy move through the cycle (figure 3). But a distinction between the ways that matter and energy move is critical to modern ecology. In theory, matter can be transferred endlessly without any loss; it truly cycles. But because some energy is dissipated during each trophic transfer, energy flows *through* the system. In other words, ecological systems require a constant input of energy, not necessarily materials. One ought not be too critical of an intellectual pioneer for failing to see all the important implications of his work. But certainly one reason why Elton failed to distinguish explicitly between matter and energy was his antipathy toward the physical sciences. The modern understanding of material cycling and energy flow rests on not only biology but also geology and chemistry. In other words, it is the study of biogeochemistry. Hutchinson was much better prepared than Elton for this kind of interdisciplinary approach to ecology.

From boyhood, Hutchinson was attracted to geology and chemistry, but his mature interest in biogeochemistry was catalyzed by reading the works of Viktor M. Goldschmidt and Vladimir I. Vernadsky.³² Goldschmidt was an important geochemist and a friend of Hutchinson's father. Hutchinson was introduced to Vernadsky's ideas by the Soviet theorist's son, a historian at Yale University.³³ Together, the younger Vernadsky and Hutchinson translated some of the father's writings and arranged to have them published in American journals. Vladimir Vernadsky's ideas were particularly important for the young limnologist. According to Vernadsky, life existed only in the *biosphere*, a thin layer composed of the upper regions of the oceans, the surface of the earth, and the lower regions of the atmosphere. Neither the term nor the idea was original, but Vernadsky's emphasis upon the cycling of chemical elements, a process that involved a close interrelationship between the living and nonliving components of the biosphere, made his work unique. Indeed, according to Vernadsky the major gases in the earth's atmosphere—oxygen, nitrogen, and

carbon dioxide—were all of organic origin. This emphasis on living organisms—the belief that *geochemistry*, in fact, ought to be *biogeochemistry*—was a major innovation with important implications for ecology. Earlier ecologists, notably Frederic Clements, had considered the relationship between biological communities and the nonliving environment. But for Clements the relationship had been one of simple physical causes and biological effects. This simple mechanistic notion of causation was being replaced by a more complex interactive concept of ecological systems, and Hutchinson's ecological studies in biogeochemistry were pioneering contributions to this movement.

Hutchinson participated in theoretical debates concerning the movement of chemical elements through the biosphere as a whole, but these forays into global biogeochemistry rested on detailed investigations of chemical cycling on a smaller scale. For about a decade and a half beginning in the mid-1930s, Hutchinson and several of his students intensively studied the history, productivity, and biogeochemistry of a small, relatively self-contained system: Linsley Pond. The relationship between Hutchinson's pond studies and his theoretical discussions of global biogeochemistry was not unlike that between Charles Elton's early studies of arctic communities and his general theoretical discussions of trophic dynamics. Both ecologists were committed to the belief that generalizations derived from the simplest ecological systems could be extrapolated to very large, complex systems. According to Hutchinson, the self-regulatory mechanisms governing the biogeochemical processes of Linsley Pond were comparable to those operating in the biosphere as a whole.³⁴

Linsley Pond, located on the outskirts of New Haven, is a small, nutrient-rich (eutrophic) lake with a surface area of about twenty-five acres and a maximum depth of about fifty feet. Beginning in 1935, Edward S. Deevey, one of Hutchinson's earliest graduate students, began studying the deep sediments that form the bottom of the lake.³⁵ Using a long boring device, Deevey removed earthen cores containing up to forty feet of sediment. The longest cores recorded nearly the entire history of the lake, beginning at the end of the last glaciation. Viewed under the microscope, samples from the core revealed the fossilized remains of tiny invertebrates, which provided a record of succession in the aquatic animal community. Identifying and counting pollen grains in the sediment revealed the successional changes in plant communities surrounding the lake and provided indirect evidence for climatic changes in the region. Hutchinson used samples from one core to analyze historical changes in the chemical composition of lake bottom.³⁶

The record of organic material was particularly significant, for it

provided a measurement of the productivity of the lake as a whole. In the very deepest samples the sediment was practically devoid of organic material, reflecting the relatively sterile condition of a newly formed glacial lake. Through time, as phosphorus- and nitrogen-containing compounds entered the lake in runoff, productivity increased. However, productivity did not increase in a simple, linear fashion. Once inorganic nutrients, particularly phosphorus, no longer acted as limiting factors for growth, productivity increased exponentially. This exponential rate of increase continued for only a relatively short period in geologic time. After the lake became eutrophic, its productivity remained essentially constant. This *trophic equilibrium* resulted primarily from the complex biogeochemical metabolism of the lake: the influx and efflux of nutrients, their cycling between water and sediment, and their movement through the food chains of the aquatic community. Trophic equilibrium was maintained until the lake, becoming a bog or marsh, ceased to be a lake.

Considering the sigmoid growth curve for productivity reflected in the historical record of sediments from Linsley Pond, Hutchinson remarked: "It is impossible to avoid qualitative comparison of this mode of development of the rate of organic production of sediment . . . to the growth curves of individual organisms and homogeneous populations."⁵⁷ Of course, there was an important difference between the development of an aquatic community and the growth of an individual organism or a population. In the latter two cases, there was a genetic continuity between either cells of the individual or generations of the population. This genetic continuity was responsible for the tendency for such systems to grow exponentially. Such a relationship did not exist within a community made up of many different, and often quite unrelated, species. Hutchinson suggested, however, that another mechanism might account for the exponential growth in productivity. During the course of succession there was a general tendency for organisms to modify the environment in such a way that it would support a greater quantity of living matter in the future. For example, nitrogen-fixing bacteria removed this important element from the atmosphere and made it available to other organisms. "Such a process," Hutchinson concluded, "would produce an effect essentially similar to that of the tendency to geometrical increase in genetically continuous systems."⁵⁸

The sigmoid curve of productivity could be interpreted as a reflection of the overall growth of the aquatic community or "biocoenosis." A similar, though not identical, pattern of development seemed characteristic of certain parts of this organic whole. For example, by counting the microfossils of the crustacean *Bosmina* in various samples

of the core, Edward Deevey discovered that the growth of populations of this invertebrate genus corresponded closely to the exponential phase of the productivity curve, though the rate of growth of *Bosmina* was greater. "In the language of the analogy between the organism and the biocoenosis," Deevey wrote, "this evidently means that a sort of allometric growth occurs, the rate of growth of the part differing from that of the whole, as the claw of the fiddler crab grows faster than the animal as a whole."⁵⁹

These rather striking suggestions that aquatic communities are like organisms should not be taken to mean that Hutchinson and Deevey were working within some sort of Clementsian paradigm. The immediate source of the ideas was probably not Clements or any other ecologist. Rather, these ideas apparently were stimulated by discussions in a seminar led by the embryologist Ross Harrison.⁶⁰ During his early years at Yale (1930-1937) Hutchinson was responsible for teaching the undergraduate course in embryology. Therefore, he and his students may have been particularly receptive to such developmental analogies.

Analogies between embryonic development and ecological succession were useful for suggesting or clarifying ecological questions, but, although they took the idea of the community as a kind of "super-organism" just as seriously as Clements did, Hutchinson and Deevey were using the organismal analogies in a much more abstract, idealized fashion.⁶¹ The truly important similarities between individual organisms and communities were at the level of mathematical equations representing energy transfer, material cycling, or growth of some biological parameter. Hutchinson, as noted at the beginning of this chapter, considered Clements's organismal analogy to be little more than a vague descriptive device. The study of succession had suffered because too much emphasis had been placed upon changes in the taxonomic composition of the community over time. These were superficial morphological changes. More fundamental, from Hutchinson's point of view, were the changes in community metabolism underlying succession. Clements had presented a physiological explanation of succession, but it was comparatively crude. By combining the biogeochemistry of Vernadsky, the trophic dynamics of Elton, and the use of mathematical models, Hutchinson and his students were creating a much more sophisticated explanation of the development and metabolism of aquatic communities.

Hutchinson's early work on the metabolism of lakes culminated in the work of his protégé Raymond Lindeman. Lindeman's contribution to the emergence of ecosystem ecology was so significant that I devote an entire chapter to his work. At this point suffice it to say that

by 1940, Hutchinson and his students had developed a distinctive approach to limnology. They were working within a general organismal framework. Although compared to Clements, they used organismal analogies in a more flexible and sophisticated manner. These analogies provided a suggestive language for discussing ongoing processes, historical changes, equilibrium, and self-regulation within the aquatic community. More important, they served as heuristic devices for suggesting mathematical explanations for ecological processes. Succession was not ontogeny, as Clements had claimed, but an equation for allometric growth might provide a common explanation for both forms of development. This abstract, mathematical theorizing became increasingly important in Hutchinson's ecology after World War II.

Circular Causal Systems in Ecology

Most of Hutchinson's early research had centered around the study of lakes, but he had also become interested in more general theoretical problems in ecology. According to Hutchinson, ecology encompassed a variety of phenomena, ranging from purely biological processes to complex chemical and physical ones. Ecological problems between these two poles could not be broken up into discrete categories, but the Yale limnologist suggested that ecology could be conveniently characterized by two broad methodological approaches.⁶² One, the *biogeochemical* mode, involved the interdisciplinary study of the movements of materials and energy through the biosphere. The second mode of ecological research was *biodemographic*. This approach was purely biological, studying numerical variations in the sizes of populations. Unifying the two approaches, according to Hutchinson, was the concept of negative feedback. Whether studying the phosphorus cycle of a lake in Connecticut or changes in the size of a population of aquatic invertebrates, the ecologist was studying self-correcting systems governed by negative feedback. This common property of ecological systems was not merely a vague, superficial similarity; there were *formal analogies* between the processes of population growth and biogeochemical cycling. In other words, regulatory mechanisms in both cases could be described by a common mathematical expression.

Hutchinson's most detailed discussion of negative feedback and formal analogy was delivered at a 1946 conference on "Teleological Mechanisms," one of a series of interdisciplinary meetings sponsored

by the Josiah Macy Foundation. These conferences were designed to present the new field of cybernetics, the study of self-regulating systems, to the broader scientific community. Participants at the meetings included a diverse group of luminaries from the fields of mathematics, anthropology, social psychology, engineering, physiology, ecology, and philosophy.⁶³ Given the diversity of the participants, the discussions at the conferences were sometimes rather amorphous. Although some participants found the meetings fruitless, many considered them worthwhile.⁶⁴ For Hutchinson, the conferences provided a stimulating intellectual environment and an unusual opportunity to synthesize his ecological ideas.

The central ideas of cybernetics—system, self-regulation, feedback, oscillation, and time lag—were used by a diverse group of intellectuals, but exactly how the ideas were employed varied greatly.⁶⁵ The core group in the new field was composed of mathematicians and other mathematically sophisticated researchers drawn from fields such as computer science and physiology: Norbert Wiener, Arturo Rosenblueth, Julian Bigelow, John Von Neumann, Warren McCulloch, and Walter Pitts. These cyberneticians were attempting to construct an overarching mathematical theory to explain the behavior of organisms, machines, and other complex systems. In fact, from the perspective of cybernetic analysis, distinctions between machines, organisms, and even societies seemed to evaporate; all three were treated mathematically as "systems." Not everyone who was attracted to cybernetics possessed the mathematical skills needed to understand fully the theory being developed by the core group. For example, the anthropologist Gregory Bateson, a regular participant at the Macy Conferences, understood little mathematics, but cybernetics offered him a set of very general concepts that could be employed heuristically or metaphorically to explore social interactions.⁶⁶

Hutchinson's use of cybernetics fell between these two extremes. Mathematically, Hutchinson was not in the same league with Wiener or Neumann, but, compared to Bateson, he was able to explore more fully the mathematical ideas developed by the cyberneticians. The Macy Conferences provided a stimulating intellectual environment within which he could apply these ideas to ecological problems. The concept of negative feedback appeared prominently in his conference paper "Circular Causal Systems in Ecology" and formal analogy, another idea central to cybernetics, formed the unifying theme of the paper. Hutchinson had employed formal analogy in his work for more than a decade. But the Macy Conference provided him with a venue for exploring, in much greater depth, its theoretical implications.

The logic of Hutchinson's "Circular Causal Systems in Ecology" combined these cybernetic concepts with the mathematical ecology created during the 1920s by Raymond Pearl, Alfred J. Lotka, and Vito Volterra.⁶⁷ The basic equation that Hutchinson employed was one originally formulated by the nineteenth-century mathematician François Pierre Verhulst and independently some seventy years later by Pearl. The Verhulst-Pearl equation describes the growth of a population within an environment containing limited resources. Using Hutchinson's notation

$$dN/dt = Nb(K - N)/K$$

where N was the population size, b represented the reproductive rate (*intrinsic rate of natural increase* in today's terminology), and K was what Hutchinson termed the "saturation level." This saturation level, today more commonly referred to as carrying capacity, is the maximum population sustainable by the environment. Without the term, $(K - N)/K$, the population grows exponentially. With the term, the population exhibits a sigmoid growth curve, approaching an asymptote at $N = K$. Biologically, the term $(K - N)/K$ reflects the fact that as a population increases it depletes resources in the environment. At least in theory, this depletion of resources reduces the rate of growth of the population. Thus, when the population is very small, $(K - N)/K$ is approximately 1, and population growth approaches the exponential growth described by $dN/dt = bN$. As the population becomes larger, $(K - N)/K$ becomes smaller, and the rate of growth continuously decreases. As $(K - N)/K$ approaches 0 growth almost ceases, and the population approaches, but never quite reaches, its saturation level (K).

Hutchinson claimed that the term $(K - N)/K$ constituted the mathematical expression for self-regulating mechanisms. Mathematically the term could be used to describe negative feedback, regardless of what biological form this feedback took. In other words, Hutchinson constructed a *formal analogy* among seemingly unrelated biological processes: individual growth, population growth, and historical changes in the productivity of an aquatic community. Clearly, the biological mechanisms causing these diverse phenomena had little in common. However, the formal analogy suggested a common method for explaining quite different ecological problems. Thus, it provided a theoretical bridge between the biogeochemical and biodemographic approaches to ecology.⁶⁸

The simple logistic equation described the behavior of biological systems approaching a stable equilibrium. However, cybernetics also

provided Hutchinson with engineering and physiological analogies for unstable systems. Cybernetics had developed largely out of the wartime problem of designing an automatic control system for anti-aircraft guns.⁶⁹ The purpose of such a device was not to aim the gun at the aircraft itself, but to direct the trajectory of the projectile toward some future position of the target. Information, in this case the difference between the present position of the gun and the future position of the target, was used to modulate the movement of the gun. Properly constructed this feedback mechanism would produce a series of dampened oscillations, swinging the gun in a smooth arc until it arrived at the proper firing position. However, if there were an appreciable delay in the feedback loop, the gun would oscillate wildly back and forth, never finding its target.

This mechanical failure in the anti-aircraft gun had a pathological analogy in neurophysiology. A patient suffering from purpose tremor is unable to successfully grasp objects because of uncontrollable oscillations of the hand.⁷⁰ Hutchinson believed that time lags in the self-regulatory mechanisms of populations might have similar effects. If there was very little lag, then oscillations would decrease as the population growth curve approached K . However, larger oscillations would appear if there was an appreciable time lag in the system:

$$dN_{(t)}/dt = bN_{(t)}(K - N_{(t-\tau)})/K$$

In this situation, rather than a smooth approach to K , the population would oscillate around the saturation level, alternately overshooting and falling below K . Such a situation might occur where the production of eggs required a significant period of time. The number of eggs released would be determined not by the population density at the time of laying (t), but rather the density at an earlier time ($t - T$) when the eggs began developing in the female's body. Like the anti-aircraft gun and the patient's hand, this population would hunt for, but never find, a stable equilibrium.

Oscillations, in any system, are potentially destabilizing. Dense populations are subject to catastrophic destruction by epidemics, and sparse populations risk extinction through random events. Therefore, Hutchinson reasoned, fluctuating populations tend to be replaced by their more stable neighbors. Natural selection, acting on various populations, improves self-regulating mechanisms by reducing time lags. As a result, most natural populations are in equilibrium most of the time.

Negative feedback mechanisms were important for not only regulating population size but also stabilizing communities. Hutchinson's

discussion of predator-prey interactions is particularly intriguing for two reasons. He attempted to put Charles Elton's idea of "automatic balanced systems" on a firm mathematical footing, and in this section of the paper he most explicitly used cybernetic concepts to bridge the biodemographic and biogeochemical perspectives in ecology.

Elton believed that predation was one of the most important mechanisms for regulating animal communities. The size of prey populations was regulated by predators, and to some extent the growth of predator populations was checked by available food. During the 1920s, Alfred J. Lotka and Vito Volterra had described such a situation in mathematical terms.⁷¹ The relationship between a predator and its prey could be described by a pair of differential equations. The rate of population growth of the prey was determined by its own natural rate of increase (b_1N_1) minus the rate at which prey were destroyed by predators. Assuming that the rate of destruction was proportional to the rate at which predators encountered prey ($p_1N_1N_2$), where p_1 was a constant that represented the efficiency of the predator, then:

$$dN_1/dt = N_1b_1 - p_1N_1N_2.$$

Assuming that the growth of the predator population was proportional to the rate at which prey were ingested ($p_2N_1N_2$) minus the natural death rate of predators (d_2N_2), then

$$dN_2/dt = p_2N_1N_2 - d_2N_2.$$

In such self-regulating systems, each population acted as a kind of mechanical governor, limiting the growth of the other population. Predators acted by influencing the death rate, but not the birth rate, of the prey. The prey acted by influencing the birth rate, but not the death rate, of the predators. Theoretically, the two populations oscillate slightly out of phase with one another.

Despite the theoretical predictions of the Lotka-Volterra model, few cases of predator-prey oscillations could be found in nature. Such oscillations could be induced in laboratory populations, but only under highly artificial conditions. Hutchinson, again, cited this negative evidence as an indication that natural selection had acted to perfect the self-regulatory machinery of the community. The oscillations inherent in the behavior of predator-prey systems had been minimized as the two populations coevolved.

The Lotka-Volterra equations could also be used to study biogeochemical cycles. A decade earlier, a little known Soviet geochemist, Vladimir Kostitzin, had used the equations to model a simple carbon

cycle involving only plants and animals.⁷² In this model, the population growth of animals was regulated by the photosynthetic production of plants, and, in turn, the population growth of the plants was regulated by the carbon dioxide liberated by the animals. In such a system, not only would the populations of plants and animals oscillate, but so too would the amount of carbon dioxide in the atmosphere. While very small oscillations in carbon dioxide levels might go undetected, Hutchinson argued that there was no evidence for significant atmospheric fluctuations. This suggested that the biosphere contained complex self-regulating mechanisms acting to maintain carbon dioxide at a constant level.⁷³

The major component of this self-regulatory apparatus was the ocean, which acted as an "enormous shock-absorber" for carbon dioxide. The ability of the oceans to absorb and release carbon dioxide to the atmosphere was mediated by a system of chemical equilibria among calcium carbonate, calcium bicarbonate, and carbon dioxide:



Carbon entered the oceans primarily from rivers, which acted as a conveyor belt carrying large amounts of bicarbonate and smaller amounts of carbon dioxide. Carbon left the oceanic reservoirs primarily through precipitation of calcium carbonate on the ocean floor and diffusion of carbon dioxide between the ocean surface and the atmosphere. A number of slower geochemical processes were also involved in the carbon cycle, but the major features of this system were exchanges of carbon among the atmosphere, oceans, and biological communities. Because the oceans contained such vast reserves of carbon, they buffered the entire system against the oscillations in carbon dioxide predicted by Kostitzin's simple mathematical model.⁷⁴

Hutchinson went to considerable lengths to justify the belief that biogeochemical cycles were self-correcting. In a section of his paper, "The Efficacy of Self-Regulating Mechanisms," he challenged the earlier claim by British geochemist G. S. Callendar that industrial combustion of fossil fuels was increasing the amount of carbon dioxide in the atmosphere. Carbon dioxide levels had increased in certain industrial regions, but, according to Hutchinson, this local phenomenon did not indicate a change in the gaseous content of the atmosphere as a whole. Furthermore, Hutchinson argued that local increases in carbon dioxide were more likely owing to deforestation in urban areas, rather than combustion of fossil fuels. He was confident that the self-regulating mechanisms of the biosphere were capable of correcting imbalances in carbon, whether natural or artificially produced.

Neither volcanos nor human industry were likely to alter the global levels of atmospheric carbon dioxide.⁷⁵

One ought not be too critical of Hutchinson for failing to anticipate a later generation's concerns about the greenhouse effect, but his 1948 discussion of the carbon cycle is striking for other reasons. It reflects his deep commitment to the concept of equilibrium. Unlike Charles Elton, who was sometimes uncomfortable with the idea, Hutchinson was convinced that nature's self-regulatory mechanisms are capable of maintaining a balance even in the face of extreme perturbations. And unlike Elton, Hutchinson emphasized the role that natural selection played in perfecting this self-regulatory machinery and maintaining it in an optimal state. From Hutchinson's perspective the population cycles that so interested Elton were "derangements" from self-regulation, deviant phenomena that could only exist under unusual environmental circumstances.⁷⁶ Hutchinson's commitment to equilibrium was certainly not unique, although it is difficult to find another ecologist who believed so deeply in the balance of nature. More unusual about Hutchinson, however, was the way he attempted to place the concept of equilibrium on a firm mathematical foundation and tried to unify theoretical ecology by drawing formal analogies between very different kinds of self-regulating systems.

Building a Research School

Students and colleagues are often almost reverential in their admiration for the "Hutchinson mystique."⁷⁷ By the time he retired in 1971, some forty doctoral students had completed their dissertations under Hutchinson's direction, and his bibliography included nearly two hundred entries covering a broad array of biological topics. Many of his students played pivotal roles in shaping the ecology of the 1950s and 1960s. Hutchinson's success as an ecologist depended upon a number of factors: location, colleagues, and scientific style. Where one is located can have an important bearing on the success of a research program. As a young biologist in his late twenties, Hutchinson joined the faculty of a prestigious university, but a university with virtually no reputation in ecology. The only other ecologist at Yale during the 1930s was G. E. Nichols, whose interest was limited to botanical topics. The zoology department, devoid of ecologists, offered Hutchinson a relatively open niche for exploring unconventional problems and novel approaches to research without worrying too much about the reactions of established colleagues. Limnology,

Hutchinson wrote to his parents soon after arriving at Yale, was "the dumping ground for inferior off-scourings of the profession of zoologists."⁷⁸ In a zoology department with an established reputation in ecology, such a marginal area of research might well have been unattractive to an ambitious, young biologist. But with the encouragement of his sympathetic chairman, Ross Harrison, Hutchinson established a somewhat unorthodox research program that eventually became a major center of ecology in the United States.⁷⁹

A great measure of Hutchinson's success was also owing to his ability to gather around him talented students and coworkers, associates who not only absorbed his ideas but modified and extended them as well. Even as a young unknown, Hutchinson was apparently able to attract and stimulate students. Gordon Riley, Hutchinson's first doctoral student, recalled: "Many students have come to Yale expressly to work with Evelyn Hutchinson. I did not. I had not heard of Evelyn before I came there. He was a young instructor—a nobody—but he was a great nobody, and the first month of his limnology course convinced me that my path lay in that direction."⁸⁰ Hutchinson's none too subtle displays of erudition irritated some students, but his enthusiasm for ecology was apparently infectious. His protégés—Raymond Lindeman, Howard Odum, and Frederick Smith—became key figures in the emergence of ecosystem ecology.

What apparently attracted many students to Hutchinson was his imaginative and innovative approach to theoretical ecology. Like most scientists, Hutchinson believed that theories should be potentially testable. However, unlike many scientists, Hutchinson believed that even false theories play a valuable role in scientific creativity. Such theories were not simply abandoned; rather, they served as raw materials for constructing new, improved theories. Even when conclusively disproved, a theory might direct the scientist's attention to previously unrecognized areas of research. Hutchinson held this view of theory construction throughout his career, but he articulated it most succinctly late in life:

even a potentially erroneous theory is an enormous advance over having no theory at all, for the incorrectness of the theory, when tested, is in a sense a measure of how far wrong are the postulates on which the theory is based. Once this has been determined, we can start modifying the theory; if we had no theory, there would be nothing to modify and we should get nowhere.⁸¹

Writing a bit facetiously, Hutchinson once described science as a "dialectical tournament" in which bold new theories entered the lists.⁸²

During the clash of ideas, many of these speculations were proven false, but the process of testing led to a deeper understanding of nature. For this reason, he argued that editors ought to be willing to publish speculative, even unorthodox, theoretical articles. On a number of occasions he actively supported younger biologists in their efforts to get controversial ideas into print. For Hutchinson, theoretical ecology was also dialectical in the broader sense that it could be seen in terms of two contrasting approaches: the biogeochemical and biodemographic perspectives. During the late 1940s Hutchinson believed that he was approaching a synthesis of these polarities through the use of formal analogy. Although this ambitious attempt to unify ecology did not succeed, it stimulated an enormous amount of creative research by his students.

Hutchinson's bold approach to theory building shared much in common with that of the young Charles Elton. However, more conservative ecologists were hostile toward what they considered Hutchinson's cavalier approach to research and his theoretical flights of fancy. Just as in his critique of Clementsian theory, Henry Allan Gleason had claimed that every species is a law unto itself, so many limnologists claimed that every lake is a unique individual. General theory, if it could be arrived at, would come only from a painstaking accumulation of facts collected from a wide variety of different aquatic systems. This extreme empiricism was common among limnologists during the pre-World War II era, and it openly conflicted with Hutchinson's approach. Chancey Juday, a prominent limnologist at the University of Wisconsin, sneered:

The Yale school of mathematical-limnologists is having a high time displaying their mathematical abilities. The interesting part about it is that they are applying mathematical formulae used in sub-atomic physics where all of the forces are presumably uniform to limnological problems where there are all sorts of un-uniform factors involved. . . . Apparently they do not have brains enough to see the point in the two very different situations. . . . In a short time I shall expect them to tell all about a lake thermally and chemically just by sticking one, perhaps two, fingers into the water, then go into a mathematical trance and figure out all of its biological characteristics. As the next stage in their evolution they will probably be able to give a lake an "absent treatment" similar to a spiritualist, so it will not be necessary to visit a lake at all in order to get its complete chemical, physical and biological history.⁵³

As we shall see in chapter 5, Juday's antagonism toward Hutchinson's style of research very nearly prevented the publication of one of the most seminal theoretical papers in ecosystem ecology: Raymond Lindeman's "The Trophic-Dynamic Aspect of Ecology."

Intellectual Foundations for a New Ecology

By the end of World War II, the intellectual foundations for ecosystem ecology were in place. Frederic Clements had hammered home the idea that the biological community, a kind of organism, developed ontogenetically. Although much modified during the post-World War II period, both the organismal and developmental aspects of Clementsian ecology became key intellectual components of the ecosystem concept. Closely related to these Clementsian ideas was the suggestion that communities have a form of metabolism. This metabolism consisted of the flow of energy and materials through the community and its surrounding environment. Although not particularly drawn to organismal analogies, Charles Elton pioneered the study of energy flow in his 1927 book *Animal Ecology*. This early attempt at trophic analysis had an important influence on later work. Indeed, energy flow became one of the two most important areas of ecosystem research after World War II. The other was the study of biogeochemical cycling. Hutchinson's influence on this area of research was manifold. He absorbed and expanded the suggestive biogeochemical ideas of V. I. Vernadsky, and he made the writings of the great Soviet scientist available to the American scientific community. Through early studies on Linsley Pond, he and his students played an important role in bringing the new biogeochemistry into ecosystem ecology. Others were doing similar research, but not within a broad theoretical framework. Hutchinson's early forays into cybernetics and mathematical theory provided the rudiments for such a framework. Cybernetics also provided a more sophisticated language for exploring the suggestive similarities between organism and ecosystem.

Lindeman's 1942 paper, "The Trophic-Dynamic Aspect of Ecology," is historically significant for a number of reasons. Robert Cook has vividly detailed the difficulties that the young ecologist encountered in his attempts to publish the paper.² These difficulties highlight the rapid and fundamental changes that were occurring within the discipline of ecology around World War II. The story is all the more dramatic because Lindeman, then twenty-seven years old, died unexpectedly as the article finally went to press. From the perspective of intellectual history the paper is important because in it Lindeman attempted a synthesis of the ideas of Clements, Elton, and Hutchinson. The result, which outraged some older, more conservative scientists, caught the imagination of a generation of post-World War II ecologists. An effective catalyst, it stimulated the rapid development of ecosystem ecology after the war. The term ecosystem had been used occasionally prior to the 1940s, but Lindeman was perhaps the first ecologist to exploit fully the concept. This chapter explores the origin of the ecosystem concept half a decade before the publication of Lindeman's classic paper, and it analyzes the way that the young ecologist used this idea to establish a new ecological specialty.

Arthur Tansley and the Ecosystem Concept

Ecosystem was coined in the mid-1930s by the British plant ecologist Arthur Tansley (figure 6).³ Because it first appeared in a strongly worded critique of Clementsian ecology, the concept has been interpreted as a radical break from Frederic Clements's idea of the organismal community. Donald Worster, in *Nature's Economy*, goes so far as to claim that Tansley's ecosystem concept owed nothing to earlier biological ideas.⁴ And Ronald Tobey, in his detailed history of American grassland ecology, characterizes Tansley's critique as a "vigorous, nearly bitter, attack" on Clementsian ecology.⁵ According to Tobey, the publication of Tansley's 1935 essay signaled the breakup of a Clementsian "microparadigm."⁶ For Tobey, Tansley serves as a kind of intellectual barometer, an indicator of the scientific acceptance of Clements's ideas. According to this interpretation, Tansley was an early supporter of Clements, but this support steadily diminished and culminated in his public rejection of Clementsianism in 1935. I share Tobey's belief in the historical importance of the relationship between Tansley and Clements; however, my interpretation of this episode is somewhat different, primarily because I am unwilling to accept

5 The Birth of a Specialty

Perhaps the most dangerous post for a referee or editor is at the boundary of a well-established discipline where a new subject is striving to be born.

—J. M. ZIMAN, *Public Knowledge:
An Essay Concerning the Social Dimension of Science*



CHARLES ELTON AND G. EVELYN HUTCHINSON played crucial roles in establishing the intellectual foundations of ecosystem ecology, but they rarely used the term *ecosystem* in their writings. Hutchinson's work, in particular, seemed to demand a new ecological unit, for he was studying complex interactions not just within the living community but also between the community and its surrounding environment. Writing in 1942, Hutchinson's protégé Raymond L. Lindeman commented that the concept of community forced a "biological emphasis" on a more fundamental set of processes.¹ At what point, Lindeman asked rhetorically, did one draw the boundary between a living community and its nonliving environment? From the perspective of biogeochemistry any such boundary was indistinct, perhaps even arbitrary. Organisms in a lake died, and their protoplasm gradually decomposed into inorganic molecules. At the same time, inorganic materials in the ooze were absorbed by living plants, incorporated into their protoplasm, and transferred through the aquatic food chains. Thus, chemical substances continuously cycled back and forth between the biotic and abiotic worlds. For Lindeman, the ecosystem concept provided a point of departure for exploring this relatively new area of ecological research. It was, he claimed, the fundamental concept in biogeochemistry.

Tobey's Kuhnian perspective on history. By presenting the history of ecology as the rise and fall of paradigms, this perspective places too much emphasis upon historical discontinuity. In chapters 2 and 3, I argued that the reception of Clements's ideas was mixed. Many leading ecologists accepted some of Clements's ideas, but rejected others; they did not accept a complete "Clementsian paradigm." In my view, Tansley exemplified this type of critical attitude. From the beginning, Tansley's enthusiasm for Clementsian ecology was tempered by considerable skepticism. And although his 1935 paper was particularly outspoken, it was not uncharacteristic from a scientist known for biting, incisive analysis. In contrast to Tobey's conclusion that this article represented a rejection of a Clementsian paradigm, my interpretation is closer to that suggested by one of Tansley's students, his biographer Harry Godwin. According to Godwin, when Tansley put forward his ecosystem concept, he was "qualifying without disabling" Clements's earlier organismal concept.⁷ My claim, in contrast to the conclusions of both Worster and Tobey, is that after World War II the ecosystem concept continued to reflect important elements of Clements's thinking. Tansley's sophisticated mechanistic view of nature also retained strong organismal overtones.

Tansley and Clements carried on a warm correspondence over the course of several decades beginning in 1905.⁸ Aside from a common interest in ecology, there was little similarity between the urbane Tansley and his more parochial American friend. Born in 1871, three years before Clements, Tansley was the product of upper middle-class Victorian society.⁹ In contrast to Clements whose serious interests were limited to botany, Tansley was a self-described dilettante. As a student at Cambridge he was a friend of Bertrand Russell, and he maintained an avocational interest in philosophy throughout his career. "If you scratch a biologist," a colleague later remarked of Tansley, "you will find a philosopher."¹⁰ As a young man he assisted the aging Herbert Spencer in revising his *Principles of Biology*. During World War I he became interested in psychoanalysis and wrote a popular book on Freudian psychology and its relationship to modern biology. This interlude in his botanical career culminated when he moved to Vienna for several months to study under Freud.

Tansley's scientific work lacked the brilliant originality of Clements's studies, but his contributions to professional ecology were nonetheless profound. As editor of *The New Phytologist*, a journal he started with his own money in 1902, Tansley promoted ecology and other new areas of botanical research. He was instrumental in establishing the British Ecological Society.¹¹ When the group was formed in 1913,

Tansley was elected president, a post that he held again during the late 1930s. For twenty years he served as editor of the society's *Journal of Ecology*. When he retired in 1937 Tansley was the most influential ecologist in Britain. This influence rested as much upon his skills as a scientific leader as on the results of his research.

Tansley's editorial duties undoubtedly sharpened his prodigious abilities as an insightful critic. According to Harry Godwin, Tansley had a unique ability to grasp new ideas and see their potential usefulness.¹² I believe that this talent, combined with his broad intellectual interests, and his leadership position within the rapidly growing discipline explain Tansley's attitude toward Clementsian ecology. He was sympathetic toward Clements's claim that a community is a kind of organism, an idea that he considered inherently useful, but he was too sophisticated to accept it completely. In a long series of critical review articles Tansley defended Clements's organismal ideas, but he also reworked these ideas into a philosophically more acceptable form. The ultimate result of this process was the ecosystem concept.

Tansley's initial foray into Clementsian ecology came in a lengthy review of Clements's first major book, *Research Methods in Ecology* (1905). The review, which appeared in his newly established journal, was written with Tansley's brother-in-law, the Cambridge physiologist F. F. Blackman. Although Clements later thanked Tansley for his "generous praise" of the book, the review had, in fact, contained much serious criticism.¹³ Blackman and Tansley considered *Research Methods* the most ambitious and important recent contribution to ecology. They were particularly impressed by Clements's discussion of ecological succession, and they were generally sympathetic to his organismal concept of the plant community: "His view of vegetation as an organism is as legitimate as the familiar idea of a human society from the same point of view. Both conceptions are useful and desirable so long as it is remembered that they are essentially analogical, that these quasi-organisms do not possess many of the essential features of real organisms."¹⁴ Clements had based his organismal theorizing on a belief that ecology was a branch of physiology: "a rational field physiology."¹⁵ His reviewers were decidedly unsympathetic toward such physiological pretensions. Indeed, Blackman nearly refused to coauthor the review because he was so "repelled" by Clements's discussion of physiology. In a letter to Tansley, Blackman complained that the entire section on physiological principles was "dreadfully crude" and "glib."¹⁶ Coming from a close friend, a scientist he deeply admired, Tansley must have taken this private dismissal of Clements's ideas seriously. However much he was attracted to

Clementsian ecology, Tansley always maintained some intellectual distance from the American ecologist. The published review of Clements's first book, a mixture of profound admiration and sharp criticism, perfectly encapsulated Tansley's attitude toward Clementsian ecology, an attitude that found expression in several articles he wrote during the next thirty years.¹⁷

Tansley was no stranger to controversy; as editor he freely expressed his opinions on a range of scientific topics. A reader, stung by one of his editorials, once accused Tansley of fomenting "botanical Bolshevism" in the pages of the *New Phytologist*.¹⁸ The comment appears ironic given Tansley's later opposition to Marxism, but it illustrates Tansley's willingness publicly to defend or criticize ideas, regardless of their popularity. During the twenty years following the publication of *Research Methods in Ecology*, Tansley promoted Clementsian ecology and he vigorously defended the organismal concept against vociferous European critics. But this does not mean that he became a disciple of Clements. In their correspondence the two men frankly acknowledged their theoretical differences, and in his public statements Tansley was equally blunt in criticizing certain aspects of Clementsian ecology. From Tansley's point of view, his American friend was arguing an extreme position, and he frequently made inexcusable philosophical errors.

To understand the origin of the ecosystem concept, it is important to consider in greater detail Tansley's critical attitude toward Clementsian ecology. Nature might be composed of aggregations of individuals, as Henry Allan Gleason argued, but Tansley responded that focusing only upon the individuals led the ecologist to ignore important biological processes.¹⁹ The ecologist had to consider the forest as well as the trees, and the idea of an organismal community drew attention to interactive processes such as succession. By emphasizing process, Clements was shifting ecology away from mere description. This, Tansley believed, was tremendously useful, for, if nothing else, it stimulated the intellectual development of the young discipline. This support for the organismal community concept was tempered, however, by Tansley's critical attitude and his philosophical training. "I . . . believe the analogy with the organism to be legitimate and useful," the British ecologist wrote, "if it is not pushed too far, and especially if we abstain from making illegitimate deductions."²⁰ The problem was that Clements did push the analogy too far and did make illegitimate deductions. Most egregiously, he often confused analogy and true identity. For Clements, succession was not just analogous to ontogeny; it was ontogeny. Because succession was a form of

development it had to be progressive; the community always matured toward a well-defined climax. Like most ecologists, Tansley rejected this claim. In some cases, which he termed *autogenic*, succession could be thought of as a developmental process. As plants successively modified the environment, the community slowly changed in an orderly manner, ultimately reaching the mature climax state. In cases of *allogenic* succession, however, fire or some other environmental factor so disrupted the process that several successional stages might occur simultaneously in the same area. Clements was quite familiar with this phenomenon, but he often ignored it in his theoretical writings. According to Tansley, one could hardly see "development" in a situation where nature was constantly in a disturbed state.

To avoid Clements's logical errors, Tansley suggested that ecologists refer to plant communities not as organisms, but as quasi-organisms. However, even this construction led to misunderstanding, and toward the end of his career Tansley proposed the more neutral term *ecosystem*. He introduced this new term in his most detailed critique of Clementsian ecology: "The Use and Abuse of Vegetational Concepts and Terms." This critical essay, which appeared in 1935, was aimed not at Clements directly, but rather at three review articles written by the South African ecologist John Phillips.²¹ Although Phillips presented a comprehensive discussion of the current state of community ecology, he made no attempt to hide his partiality to Clements's ideas. At the conclusion of the final article, Phillips "earnestly" invited criticism from his readers.²² For Tansley, with his keen analytical mind and critical temperament, Phillips's request amounted to throwing down the gauntlet.

Clements proudly claimed that Phillips's articles presented the organismal concept to a new generation of ecologists.²³ But from Tansley's point of view, the young South African exemplified the worst features of Clementsian ecology. In his articles, Phillips blatantly stepped over the line that separated useful analogy from dangerously misleading ideas. According to Tansley, "Phillips' articles remind one irresistibly of the exposition of a creed—of a closed system of religious or philosophical dogma."²⁴ Hyperbole notwithstanding, there was much in Phillips's papers that offended Tansley's basic scientific beliefs. For Tansley, the scientist had to be pragmatic, always willing to modify or reject concepts when they were found wanting, but Phillips fairly bubbled over with uncritical enthusiasm for holistic organismism, claiming that "it has become to me the deepest and most abiding reality, paradoxically both a starting point and a goal in the scientific study of communities."²⁵ With the same uncritical zeal, Phillips

derived illegitimate deductions from the organismal concept, restating Clements's threadbare claim that succession was always progressive. This must have been particularly irritating to Tansley, given the distinction between autogenic and allogenic succession that he had made so carefully a decade earlier. Rather than providing a detailed refutation of Tansley's distinction, however, Phillips blithely stated that Clements and his followers refused to recognize the existence of allogenic succession. Given such a transparently partisan position, there was some justification for Tansley's acerbic claim that Phillips's entire discussion of succession rested upon an article of faith: the community is an organism; therefore, it *must* develop to a single, adult form.

Tansley was also critical of Phillips's organicism on more general philosophical grounds. In the final article of his series, Phillips allied his organismal ideas with the philosophy of biology presented in Jan Smuts's inscrutable *Holism and Evolution*.²⁶ This was a significant change in Clementsian ecology, for in his early writings Clements had rarely explored the broader philosophical implications of his organismal ecology. Prior to the 1930s he apparently was unfamiliar with the holistic organicism of biologists such as John Scott Haldane and William Morton Wheeler. And on the face of it, Clements's mechanical-organic theory of succession fit uncomfortably with Smuts's passionately antimechanistic defense of emergent evolution. Furthermore, Smuts specifically denied that the organismal community, at least in human sociology, was anything more than a figure of speech.²⁷ Nonetheless, by 1935 Clements was avidly recommending Smuts's book to his colleagues, and both he and Phillips were using holism as a philosophical justification for their organismal ecology.²⁸

Tansley objected to holism on almost every point, objections shared by several other critics of Smuts's book.²⁹ For Tansley, Smuts's claim that the properties of a whole cannot be predicted from those of its parts amounted to intellectual defeatism. An example of such emergent properties, one used by Smuts and Phillips, was that the properties of a water molecule cannot be predicted solely from the properties of hydrogen and oxygen atoms. To this, Tansley retorted, "who will be so bold as to say that this new entity, for example the molecule of water and its qualities, would be unpredictable, if we really understood *all* the properties of hydrogen and oxygen atoms and the forces brought into play by their union? Unpredictable by us with our present knowledge, yes; but *theoretically* unpredictable, surely not."³⁰ To dogmatically assert that reductionistic explanations were invalid amounted to slamming the door on a potentially fruitful ap-

proach to scientific research. Smuts's claim that the whole was more than the sum of parts was also objectionable to Tansley because the term *sum* was so vague. Indeed, Smuts's entire discussion of holism and its application in the sciences was marked by a singular lack of clarity. Given his penchant for logical analysis, Tansley must have found deciphering the meaning of holism a trying experience. Too often Smuts's writing degenerated into numbingly repetitive jargon: "The whole-making, holistic tendency, or Holism, operating in and through particular wholes, is seen at all stages of existence."³¹ The claim that this nebulous holism was a "creative force" was dangerously misleading. In a certain sense, Tansley admitted, a community of plants (a "whole") might be said to be the cause of its own development, but this really meant nothing more than that under certain circumstances succession resulted from the collective activities of a set of individual plants. There was no "holistic tendency" at work in succession, only specifiable interactions among individuals and between these individuals and the physical environment.

The intensity of Tansley's attack on Phillips's holism may have reflected deeply held political and social beliefs, a historical interpretation suggested by Ronald Tobey.³² An admirer of Herbert Spencer, Tansley was deeply committed to individualism.³³ In his early writings, Clements rarely explored political or philosophical issues. However, during the 1930s, he began to espouse a collectivist view of society. Decrying the "myopic individualism" that he considered responsible for the tragedy of the Dust Bowl, Clements applauded the social engineering of the New Deal.³⁴ Society was a huge organism greater than the sum of its parts; its efficient operation required extensive social integration directed by an elite group of technical experts. Within the intellectual context of the 1930s, there was nothing particularly original or profound in Clements's social views,³⁵ but they touched a raw nerve in Tansley. Collectivism was abhorrent to him; beneath its biological veneer, the holism espoused by Smuts, Clements, and Phillips embodied an objectionable political philosophy.³⁶

Tansley's students have vigorously denied that his scientific views were shaped by political or philosophical beliefs. It is certainly true that Tansley's ecological ideas developed many years before his involvement in the Society for Freedom in Science and his public statements against Marxist totalitarianism during World War II.³⁷ Furthermore, when it suited his philosophical purposes, Tansley used the ideas of prominent Marxist thinkers. Tobey's interpretation, however, cannot be rejected out of hand. Tansley's writings reveal a man who refused to distinguish sharply between biology and political

philosophy. More than most ecologists of his day, Tansley was willing to draw analogies between nature and human society. There may have been no direct cause-and-effect relationship, but it seems reasonable that the ecosystem concept developed partly as a result of Tansley's impatience with the social implications of holistic organicism.

Despite his devastating critique of Phillips's ideas, Tansley never completely broke with the organismal concept. As he had several times before, Tansley restated his belief that important analogies existed between organisms and communities. The problem, as he had repeated so often, was that Clements (and now Phillips) pushed the analogies too far. They continued to insist that communities were not simply like organisms but that they were, in fact, organisms. This intransigence was impeding the growth of ecology. Tansley, therefore, proposed the ecosystem as an alternative concept that would avoid the excesses of Clementsian ecology without sacrificing the inherent usefulness of the organismal concept. As Tansley later acknowledged, one could still consider the ecosystem to be like an organism, but such a belief was not necessary.³⁸ Indeed, Tansley seemed to prefer a concept with a pronounced flavor of modern physics.

Tansley based his new ecosystem concept on the philosophy of Hyman Levy, a prominent British Marxist and mathematical engineer. According to Levy, the universe is composed of partially overlapping systems. "Science," Levy argued, "like common sense, sets out in the first instance to search for systems that can be imagined as isolated from their setting in the universe."³⁹ These mental "isolates," which always corresponded to some physical reality, could be expanded or reduced according to purposes of the scientific analysis. For example, for the purposes of anatomy, a tree could be considered a well-isolated biological system, but for the physiological purposes of understanding photosynthesis or growth, the system needed to expand to also include some elements of the physical environment.⁴⁰

Levy's *The Universe of Science* presented a picture of science similar to the more fragmentary one that Tansley had accepted throughout the 1920s and 1930s. Because nature was so complex, ecologists were forced to focus on only certain aspects of "kaleidoscopic" reality.⁴¹ In an important sense, communities and ecosystems were natural objects, for they corresponded to something real in nature; but they were also abstractions, isolated from the welter of sense experience. "Actually the systems we isolate mentally are not only included as parts of larger ones," Tansley argued, "but they also overlap, interlock and interact with one another. The isolation is partly artificial, but is the only possible way in which we can proceed."⁴² This meth-

odological statement was tremendously significant for the future of ecology. It freed the ecologist from the rigid organismal concept advocated by Clements. One could still draw useful analogies between organisms and ecosystems, but there was no reason to believe that the ecosystem really was a type of organism. Tansley's innovation also freed the ecosystem concept from a rigid geographical basis. The concept of community, as a geographically defined entity, had become mired in controversy. What were the natural boundaries of communities? Were communities local associations of plants, or did they extend over climatic regions? These controversies had been incessant and inconclusive, but the ecosystem concept made them irrelevant. Ecosystems were not completely arbitrary; for example, a lake might have fairly well-defined boundaries. Even in situations where obvious boundaries did not exist, however, the ecologist could define them for the purposes of research.

Tansley was not an experimental ecologist, and apparently he was only dimly aware of the possibilities implied by his new concept. But G. Evelyn Hutchinson recognized the necessity of isolating systems, perhaps even arbitrarily, to measure the transfer of energy and matter across their boundaries. This experimental approach was used with great success in fields such as thermodynamics, biochemistry, and physiology, and by the end of the 1930s Hutchinson saw that it could also become the starting point for a new ecology.⁴³ Within half a decade, Raymond Lindeman set the course for this new ecology.

Raymond Lindeman and a New Direction for Ecology

Raymond Lindeman was an earnest young man (figure 7). "I don't believe I ever saw him laugh or smile," recalled a friend. "He was subject to stomach ulcers. . . . He was so intense with his field studies that sometimes he would work until he began to vomit blood."⁴⁴ That recollection may be overly severe, but by all accounts Lindeman became almost totally immersed in his research. As a high school student applying to Park College in Missouri, he expressed a desire to become an experimental biologist. He had considered law as a more practical alternative, he wrote, but had given up this "passing fancy" for his first ambition—science. Despite the financial attraction of law, a life in science provided a greater opportunity to serve humanity, and it allowed one to "see and try to understand the majestic symmetry of the universe."⁴⁵ This was not simply an exaggerated expression

of youthful idealism. Growing up during the Great Depression, the son of a struggling Minnesota farmer, Lindeman knew the value of a dollar. Rather, this early statement spoke to a deeper idealism and commitment to science, personal characteristics that made a deep impression on those who knew him.⁴⁶

After graduation from Park College in 1936, Lindeman studied limnology under Samuel Eddy at the University of Minnesota. Eddy was a competent, but not particularly distinguished, scientist. Of greater importance to Lindeman's intellectual development was the plant ecologist W. S. Cooper, a student of Henry Chandler Cowles. In his plant ecology courses, Cooper presented a broad historical overview of the field. The leading figures in the field, from the late nineteenth century on, were discussed and their ideas criticized. Lindeman took copious notes during Cooper's lectures and later highlighted the important points with colored pencil.⁴⁷ These theoretical issues were also discussed in a more informal setting when graduate students met regularly at the Cooper home.⁴⁸ Thus, by the time that he finished his graduate studies, Lindeman was not only trained as a limnologist, but, under Cooper's tutelage, he had also been exposed to the major conceptual developments shaping pre-World War II plant ecology. "These ideas, particularly the concepts of succession and climax community, held an important place in Lindeman's later theoretical writings."

Lindeman came to Hutchinson's laboratory in September 1941 on a Sterling postdoctoral fellowship. The fellowship year, shortened by his death in June 1942, was a remarkably creative period for Lindeman. His brief association with Hutchinson resulted in a classic paper, "The Trophic-Dynamic Aspect of Ecology." In this paper Lindeman used the new ecosystem concept to create a synthesis of ecological principles derived primarily from Clements, Elton, and Hutchinson. The paper formed the cornerstone for much post-World War II ecosystem ecology. Initially, however, Lindeman's theoretical approach met with considerable skepticism and hostility from several leading ecologists. The manuscript was originally rejected by the editorial board of *Ecology*, and only through Hutchinson's intervention was it finally accepted by that journal.⁴⁹ The story is all the more poignant because Lindeman died from a congenital liver ailment shortly before his paper appeared in print.

Great research and great teaching do not necessarily go together, but in the case of Hutchinson the two activities meshed perfectly. One key to his success was his ability to attract imaginative young biologists to his laboratory and to stimulate their intellectual development. What often resulted from these collaborations were highly original

theoretical works woven together from ideas provided by both teacher and student. No case illustrates this form of collaboration so clearly as Lindeman's article on trophic dynamics.⁵⁰ In this paper Lindeman credited Hutchinson with providing many key concepts that he used in his theoretical discussion of limnology. A superficial reading of the paper might give the impression that the truly original parts of the paper were Hutchinson's rather than Lindeman's. But archival evidence suggests a very different interpretation. Writing the paper involved a complex development of ideas, ideas that neither man had fully worked out before Lindeman arrived at Yale.

One can trace the development of these ideas by comparing Lindeman's dissertation and the successive drafts of the trophic dynamic paper.⁵¹ Analyzing Hutchinson's influence on this development is complicated by the fact that Lindeman was quite familiar with Hutchinson's work when he was writing his dissertation in Minnesota. Throughout this period (1939-1941) Lindeman corresponded frequently with Hutchinson's student Edward Devey and somewhat less frequently with Hutchinson himself. This correspondence reveals that Lindeman began thinking deeply about Hutchinson's approach to ecology well before he arrived in New Haven. If Lindeman wrote anything during his "pre-Hutchinsonian" period, it apparently no longer exists.

Less directly, the historian can ask what each man brought to the relationship. By 1941, Hutchinson had spent a decade studying the biogeochemistry of Linsley Pond. He was beginning to establish his reputation as one of the leading limnologists in the United States, and he was sufficiently confident of his position within the specialty that he had begun writing a general treatise on limnology.⁵² He had also taken very preliminary steps toward outlining a mathematical explanation for energy flow. Each trophic level could be characterized by its energy content, which changed as energy entered and left. Therefore, a complete explanation of community energetics consisted of a series of differential equations representing movements of energy into and out of the various trophic levels. His sketchy notes formed a suggestive beginning, but as Hutchinson admitted, it was hardly a theory: "At present it is merely possible, introducing certain assumptions of a more or less arbitrary nature, to obtain approximate values in the very simplified equations that result."⁵³

There is no reason to believe that Lindeman contributed directly to the development of Hutchinson's mathematical concepts. His background in mathematics amounted to no more than courses in trigonometry and college algebra and perhaps a graduate course in statistics.⁵⁴ Indirectly, he undoubtedly contributed a great deal, for he

brought with him a wealth of information about trophic relationships in aquatic systems. As a graduate student Lindeman had spent five years studying a senescent lake in central Minnesota: Cedar Lake Bog. His dissertation dealt broadly with the geological, physical, chemical, and biological characteristics of the lake.⁵⁶ Most of the work focused, however, upon the food web in the lake. Prior to 1941 Hutchinson had not studied the trophic relationships in Linsley Pond in any detail. Thus Lindeman provided him with a fund of knowledge and field experience necessary for building a mathematical theory. Lindeman, in turn, used Hutchinson's nascent mathematical concepts to develop a very general theory of energy flow in ecosystems. He had begun to explore these ideas in a tentative and qualitative manner in the final chapter of his dissertation. During his brief stay at Yale, he found the mathematical tools to do so in a much more rigorous fashion.

In the opening paragraphs of his article, Lindeman presented the "trophic-dynamic viewpoint" as a new, more fundamental approach to ecological problems. Earlier ecologists, according to Lindeman, had emphasized the taxonomic composition of communities; they had described either the static distribution of species or the changes in species during the course of succession. Repeating a criticism that Hutchinson had previously voiced, Lindeman argued that these earlier approaches—what he referred to as the "static species distributional viewpoint" and the "dynamic species distributional viewpoint"—drew an unnatural dividing line between the living community and the nonliving environment.⁵⁶ Biogeochemistry was obliterating this arbitrary distinction; energy and materials were constantly moving back and forth across the often indistinct boundary separating the organic and inorganic worlds. "This constant organic-inorganic cycle of nutritive substance is so completely integrated," Lindeman argued, "that to consider even such a unit as a lake primarily as a biotic community appears to force a 'biological' emphasis upon a more basic functional organization."⁵⁷ This more basic functional organization was found at the level of the ecosystem, a "system composed of physical-chemical-biological processes active within a space-time unit of any magnitude."⁵⁸ Taking Tansley's skeletal concept, Lindeman fleshed it out. He took Charles Elton's older trophic dynamic theory, which had focused almost entirely upon the living community, and, using the newer concept of ecosystem, he gave this theory a biogeochemical interpretation.

Elton's early trophic theory had traced the movement of *food* through the living community, and in his earlier writings Lindeman

accepted this general explanatory scheme. After arriving at Yale and reading Hutchinson's lecture notes, Lindeman began to distinguish more clearly between *energy* and *matter*. This important conceptual refinement is clearly revealed in the food cycle diagrams that Lindeman included in his early publications.⁵⁹ Chemical substances underwent constant cycles of synthesis and degradation. Simple inorganic compounds were synthesized into complex organic molecules by photosynthetic organisms, the *producers* of the ecosystem. These organic molecules underwent further chemical transformations as they moved through food chains composed of herbivores and carnivores, the *consumers* of the ecosystem. Ultimately, all these complex organic molecules were degraded again to simple inorganic substances by the action of bacteria and other *decomposers* in the ecosystem.

Driving this cyclic process was a one-way flow of energy. Solar energy was captured during photosynthesis and transformed into chemical energy stored within organic molecules. Through the process of predation this chemical energy was transferred from one trophic level to the next, but at each step some was converted into kinetic energy or otherwise dissipated to the environment. Thus, not all chemical energy stored in a trophic level could be transferred to the next higher level. This was of fundamental importance because it meant that, unlike matter that could be recycled through the ecosystem, a constant flux of energy was necessary to keep the ecosystem operating. This realization also suggested a more fundamental solution to an important biological question that Charles Elton had tentatively answered a decade and a half earlier: Why is the number of trophic levels in a food chain generally limited to four or five?

Elton had answered this intriguing question in terms of the size and numbers of organisms. As one moved up the food chain, animals tended to become larger and fewer in number. At some point, generally around the fourth or fifth step in the chain, the surplus food produced by a trophic level was no longer able to support another group of even larger predators. Lindeman solved this problem more elegantly by reducing it to a physical explanation in terms of energy: "the energy of no food level can be completely extracted by the organisms that feed upon it."⁶⁰ Formally, one could represent this relationship among trophic levels by a series of terms:

$$\lambda_0 > \lambda_1 > \lambda_2 \dots > \lambda_n$$

where the productivity, λ_n , represented the energy transferred to a trophic level from the next lower level. As one moved up the food

chain, productivity decreased at each step. Thus, Lindeman had reformulated Elton's pyramid of numbers into a pyramid of energy. Available energy decreased at each successive level in a food chain. At some point, generally the fourth or fifth level in the chain, the amount of energy was insufficient to sustain another population of predators.

Why did productivity decrease at each successive trophic level? Each trophic level (n) contained a quantity of energy (Λ_n). Energy entered the trophic level at a rate (λ_n), which Lindeman had defined as the productivity of level n . At the same time energy was lost at a rate (λ_n). But this energy loss from trophic level n was not the same as the energy that entered the next trophic level (Λ_{n+1}). In fact, it was always greater. Much energy was dissipated from trophic level n as a result of metabolism. Although this respiratory heat constituted a loss of energy from the quantity Λ_n , it did not constitute a gain in Λ_{n+1} . Furthermore, some organic matter consumed by the predators in level $n+1$ was not assimilated. Wood, hair, bone, and other relatively indigestible substances contain calories, but not in a form usable by most animals. Again, these calories constituted a loss from Λ_n , but they did not contribute to Λ_{n+1} . Finally, some members of trophic level n died of nonpredatory causes. These calories were transferred immediately to decomposers, not to the consumers at trophic level $n+1$.

Although Lindeman did not use such pictorial representations in his paper, one can visualize the energy budget for trophic level n as a simple input-output system, with the energy input always exceeding the useable output to the next higher level. Each trophic level is a "black box" containing a quantity of energy (Λ_n). Energy flows into the box at the rate (λ_n) and flows out of the box at a rate (λ_n). Not all this energy flows, however, into the box representing the next trophic level; λ_n is always greater than λ_{n+1} . The difference represents either energy lost as heat or energy in a form unusable by organisms in trophic level $n+1$. This type of black box diagram became a standard method of representing trophic dynamics during the decades following World War II (figure 8).

Lindeman's formulation posed a number of intriguing questions. For example, how do the productivities of the same trophic level in different ecosystems compare? And within the same ecosystem, is the efficiency of energy transfer between any two successive trophic levels (i.e., $\lambda_n - 1/\lambda_n$) a constant, or does it vary? Providing answers to such questions was central to understanding both how ecosystems function and perhaps how to exploit them economically. Elton had suggested

that all ecosystems share a common trophic "ground plan"; Lindeman's paper suggested how this ground plan might be quantitatively studied. For young ecologists entering the field after World War II this was an exciting prospect.

The final section of Lindeman's paper was the most speculative, for here he attempted to unite succession, a central concept in pre-World War II ecology, with the newer study of energy flow. His discussion of succession was heavily influenced by both older Clementian notions of development and Hutchinson's developmental metaphors for productivity in Linsley Pond. A few years before meeting Lindeman, Hutchinson had suggested that as a lake aged productivity followed a logistic pattern of growth, reaching what he referred to as "trophic equilibrium" when the lake became nutrient-rich, or eutrophic. In the original draft of his paper, Lindeman expanded on this Hutchinsonian idea by portraying succession as a series of such sigmoid curves. Each stage in succession, from lake to bog to forest, was accompanied by an increase in productivity. Productivity increased exponentially at first, but then plateaued as the system reached a new "stage equilibrium." This successive pattern of logistic growth continued until a climax forest was established and productivity was maximized. Lindeman and Hutchinson presented this successional scheme at the annual meeting of the Ecological Society of America in Dallas, and the younger ecologist later acknowledged that it came as "a rude shock" when he was informed that there was no empirical support for his simple growth curves for productivity.⁶¹ After some tinkering, he settled on a less elegant graph. In the published version, one can still see the remnants of the original sigmoid curves. But the transition from aquatic to terrestrial succession is marked by a dramatic decrease in productivity, and productivity also decreases slightly at climax.

As Lindeman readily admitted, his attempted synthesis of succession and energetics, based on meager data, was necessarily tentative; however, it foreshadowed a number of more sophisticated discussions of the energetic basis of succession.⁶² And the evolution of this section of the paper is intriguing for the glimpse it provides of Lindeman's creative imagination. His first impulse was to envision succession as a progressive, developmental process leading to a climax state. This reflected the modified Clementian ideas that he had been taught by W. S. Cooper at the University of Minnesota.⁶³ It also reflected Hutchinson's view that succession was a developmental process leading to a stable equilibrium. Following Hutchinson's lead, Lindeman idealized this process by using a simple mathematical formula, the logistic equation.

But Lindeman was neither a dogmatic Clementsian nor a detached theoretician. When he realized that his original explanation could not be supported by empirical evidence, he was willing to abandon it—but not completely. In true Hutchinsonian fashion, he used elements of the falsified scheme to produce a more realistic picture of succession.

Lindeman and His Critics

Ecosystems, productivities, and trophic levels have become so embedded in the language of modern ecology that it is difficult for the modern reader to recognize just how revolutionary Lindeman's paper appeared in 1942. It stands as one of the great intellectual watersheds in the history of ecology. On one side of this divide stood a small group of mostly younger ecologists who rather quickly grasped the significance of Lindeman's accomplishment. The publication of his paper was followed by a flurry of similar attempts to refine, clarify, and expand trophic concepts.⁶⁴ These, together with important field studies, were largely responsible for the early development of ecosystem ecology after World War II. On the other side of this intellectual watershed stood a larger group of ecologists, older and well-established in the field, who had little appreciation of Lindeman's accomplishment.

Two months after arriving in Hutchinson's laboratory, Lindeman submitted his paper for publication in the journal *Ecology*.⁶⁵ The responses from two anonymous reviewers, now believed to have been Chancey Juday and Paul Welch, were extremely negative.⁶⁶ Welch, a professor at the University of Michigan and author of a highly respected textbook on limnology, complained that the paper was too speculative and lacking in empirical evidence; in short, it was a "desk produced" essay, rather than a true piece of scientific research. "What limnology needs now most of all," Welch concluded, "is research of the type which yields actual significant data rather than postulations and theoretical treatments."⁶⁷ Juday, a biologist at the University of Wisconsin and perhaps the leading limnologist in the United States, was even more condemnatory. As discussed in chapter 4, Juday was bitterly opposed to the mathematical ecology of Hutchinson and his students. His commentary on Lindeman's paper dripped with sarcasm: "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."⁶⁸ "According to our experiences," Juday continued, "lakes are '*rare individualists*' and are *very stubborn* about fitting into mathematical formulae and artificial schemes proposed by man."

Thomas Park, the editor of *Ecology*, was placed in a quandary. He found Lindeman's paper stimulating but was reluctant to publish the manuscript over the strident objections of two eminent limnologists. With "some reluctance and distress," Park wrote Lindeman that he was forced to reject the paper.⁶⁹ Almost immediately, Hutchinson, in a three-page letter to Park, defended Lindeman's theoretical approach and rebutted the referees' criticisms. Park sent copies of this letter to Juday and Welch, who, after reading it, restated their strong opposition to publishing Lindeman's paper. Faced with this impasse, Park allowed Lindeman to resubmit the paper, which he then turned over to his colleague at the University of Chicago, Warder Clyde Allee. Allee, unenthusiastic about the paper, was not strongly opposed to having it published. Despite this lukewarm response from a third referee, Park decided to accept the paper. "I rather imagine that the original referees will still object to certain of its basic premises," he wrote Lindeman, "but I think it best to publish your paper regardless. Time is a greater sifter in these matters and it alone will judge the question."⁷⁰

During the negotiations over his paper, Lindeman suffered an attack of jaundice, a disease he also had suffered from as a graduate student. His health deteriorated rapidly during the spring of 1942 and following surgery he died on June 15. Four months later, his trophic-dynamic paper appeared in *Ecology*.

The initial negative reactions to Lindeman's paper reflect resistance to fundamental changes occurring in ecology, changes that closely accompanied the birth of the new specialty of ecosystem ecology. As Robert Cook has pointed out, much antipathy toward Lindeman's work stemmed from a strong mistrust of mathematical theory.⁷¹ This aversion to mathematics is clearly evident both in Juday's review of Lindeman's article and his other vitriolic attacks on the Hutchinson school.⁷² But more was at issue here than mathematics. Juday was a leader of the most prestigious limnological research group in the United States. Philosophically he was a strong empiricist, leery of all general theories—mathematical or not. The Hutchinson school was much smaller, but it was rapidly gaining influence. Both the philosophical differences and the rivalry between the two groups is evident

in the sarcastic jokes that circulated privately in the two competing laboratories. Juday derided the Hutchinson team for analyzing lakes by dipping a finger or two into the water.⁷⁴ Hutchinson's students condescendingly remarked that Juday's team was capable of making ten thousand measurements without having a single idea.⁷⁵ Inevitably, the two groups viewed Lindeman's paper differently.

From the perspective of Juday and Welch, Lindeman's paper was speculative because it attempted to draw broad generalizations from a rather limited body of data. Lindeman had relied primarily upon his own detailed study of Cedar Lake Bog, but he also referred to several other limnological studies, including one by Juday. This was not enough for the Wisconsin limnologist. Lakes were "rank individualists," Juday claimed, resistant to theoretical generalizations. Understanding limnology could only come from the gradual accumulation of data gathered from many different lakes, a painstaking empirical process that Juday had begun several years before Lindeman was born. Other biologists agreed. Although he wrote a sympathetic letter to Hutchinson after Lindeman's death and expressed enthusiasm for the general thrust of the young scientist's research, Charles Elton later complained that Lindeman's calculations were "guesses rather than reliable facts. . . . His conclusions are, to say the least, a shot in the dark."⁷⁶

In marked contrast to Juday's "bottom-up" approach to ecological research, Hutchinson and Lindeman saw a much more creative role for theory. Linsley Pond and Cedar Lake Bog were model systems from which general explanatory principles could be derived. These principles could be empirically tested, but even if they eventually turned out to be false they served as useful guides to further research. Both men believed that this justified publishing the trophic-dynamic paper. In a letter to W. S. Cooper, Lindeman admitted that his theoretical work had a rather shaky empirical base. "I have a feeling, though," he wrote, "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."⁷⁸ "Even should none of his [Lindeman's] generalizations ultimately hold," Hutchinson wrote Park after the manuscript's rejection, "the work of disproving them will provide important information that would probably be obtained in no other way."⁷⁷ From the perspective of Juday and Welch, Lindeman's desk-produced paper was taking up space in a journal that ought to be devoted to hard data. But from the

perspective of Lindeman and Hutchinson, the speculative paper served as both guide and stimulus for future research.

With historical hindsight it is easy to see Lindeman's paper as the major point of departure for post-World War II ecosystem ecology,⁷⁸ but both Welch and Juday failed to recognize Lindeman's role in establishing a new specialty. Their failure to do so is perhaps not too surprising. Juday had constructed energy budgets for Wisconsin lakes, but he had never attempted to place these within a broader theoretical framework. Others, notably Edgar Transeau at Ohio State University, had taken a more theoretical approach to ecological energetics. However, Transeau had limited his discussion to the accumulation of energy by plants, what is now referred to as primary productivity.⁷⁹ Charles Elton and the German limnologist August Thienemann had independently introduced the concept of trophic levels several years earlier.⁸⁰ But what most clearly distinguished Lindeman from older ecologists was his use of the ecosystem concept. With this concept he was able to synthesize elements taken from traditional studies in fisheries biology and limnology, the newer biogeochemical approach to studying lakes, Elton's terrestrial animal ecology, and traditional plant ecology.

Lindeman himself believed that he was working within the "Eltonian tradition."⁸¹ But, as Elton's lukewarm reaction to the later developed ecosystem ecology suggested, Lindeman's approach differed significantly from the British ecologist's "scientific natural history." The ecosystem concept was better suited to the type of highly abstract theorizing that Lindeman and Hutchinson employed. Lakes, streams, forests, or coral reefs could all be treated as idealized systems composed of trophic levels. Each trophic level was a kind of black box through which energy and materials moved. Indeed, as Hutchinson noted in a postscript to the trophic-dynamic paper, Lindeman had reduced all the biological complexity of Cedar Lake Bog to energetic terms. Although he had barely sketched the outlines of this new energetic approach to ecology, its explanatory power seemed obvious enough. Why are trophic levels in ecosystems usually limited to four or five? In 1927 Charles Elton had proposed an answer to this intriguing question in terms of the relative size and numbers of various animals. For Lindeman a more elegant and fundamental explanation could be provided in terms of energy. Critics later complained that Lindeman's followers were "obsessed with calories."⁸² But during the postwar decades the study of energy flow appeared to be of fundamental importance for understanding ecosystems.

Theoretical Foundations for a New Ecology

Arthur Tansley proposed the ecosystem concept as a more acceptable substitute for Frederic Clements's idea of the community as a complex organism. But neither Tansley nor Lindeman completely severed the ties between the older and newer concepts. With some qualifications, the idea of succession as a developmental process was an integral part of Lindeman's argument. Even more important, he borrowed Hutchinson's idea that energy and material transfer within aquatic systems constituted a kind of "metabolism." These were useful analogies, but they were no more than that. Like Hutchinson, Lindeman used organismal analogies as heuristic devices in developing theories. The mathematical theory, not the similarities between organisms and lakes, was truly important. The ecosystem concept was well-suited for this new type of study. Once the ecologist had delimited the system, the movements of energy and material within it could be measured.

Lindeman criticized earlier ecologists for taking a too biological perspective on their work. In important ways Lindeman removed the traditional biological orientation from ecology. This shift is particularly striking when one compares the new approach to trophic dynamics with the older ideas of Elton. Elton's ideas of food chains and niches were firmly rooted in natural history; he always seemed to have specific animals in mind when he discussed these theoretical units. But in the newer approach, species and populations seemed to evaporate. When considering biogeochemistry, V. I. Vernadsky had claimed, "the single living organism recedes from view: the sum of all organisms, *i.e.* living matter, is what is important."⁸⁵ Hutchinson and Lindeman took much the same view as the influential Soviet geochemist. Trophic levels did not correspond exactly with populations or species; a given species might simultaneously act as both herbivore and carnivore. From the perspective of the ecosystem this made little difference. In theory, a species's metabolic activities could be appraised among several different trophic levels. Following this approach, however, trophic levels ceased to be truly biological units; instead, they became black boxes, idealized mechanisms for channeling and dissipating energy.

From one perspective Lindeman had deemphasized biology, but from another perspective ecosystem ecology became more biological than its predecessors. The split between botanists and zoologists was a

prominent feature of pre-World War II ecology. Bacteria, fungi, and other "lower forms" of life were barely considered. Frederic Clements and Victor Shelford had made an initial attempt at synthesis in their 1939 book, *Bio-Ecology*. But ecologists of a younger generation found the book uninspiring. Lindeman's emphasis on energy flow focused attention on the unity of the ecosystem. Ecology was about more than animals or plants in isolation; it was about the interactions of various groups. Producers, consumers, and decomposers all played important functional roles within the ecosystem. For ecologists after World War II, the ecosystem promised a means for unifying what had previously been a discipline sharply divided along the boundary between zoology and botany.⁸⁶

How important can a single paper be in establishing a new scientific specialty? Unlike other ecologists who studied productivity and trophic relationships, Lindeman placed his ideas within a coherent conceptual framework. Discussing his research within the context of the ecosystem allowed Lindeman to generalize rather broadly. The paper was not simply about lakes; it applied equally to all ecosystems, terrestrial or aquatic. Many of Lindeman's ideas were speculative, but this in itself encouraged constructive criticism. Finally, the drama surrounding the publication of the paper and Lindeman's tragic death focused considerable attention on his work. For all these reasons, "The Trophic-Dynamic Aspect in Ecology" became a catalyst for the development of ecosystem ecology. As we see in chapter 6, a number of social factors also encouraged this development.



Figure 1.
Henry Chandler Cowles, 1913 (negative no. DN 60,959, Chicago
Historical Society).



Figure 2.
Frederic Clemens, 1914 (American Heritage Center, University of Wyoming).

Figure 3.
Charles Elton (*center*) with Aldo Leopold (*right*) and the Canadian ornithologist William Rowan (*left*) at the Matamek Conference on Population Cycles, Labrador, 1931 (University of Wisconsin Archives).



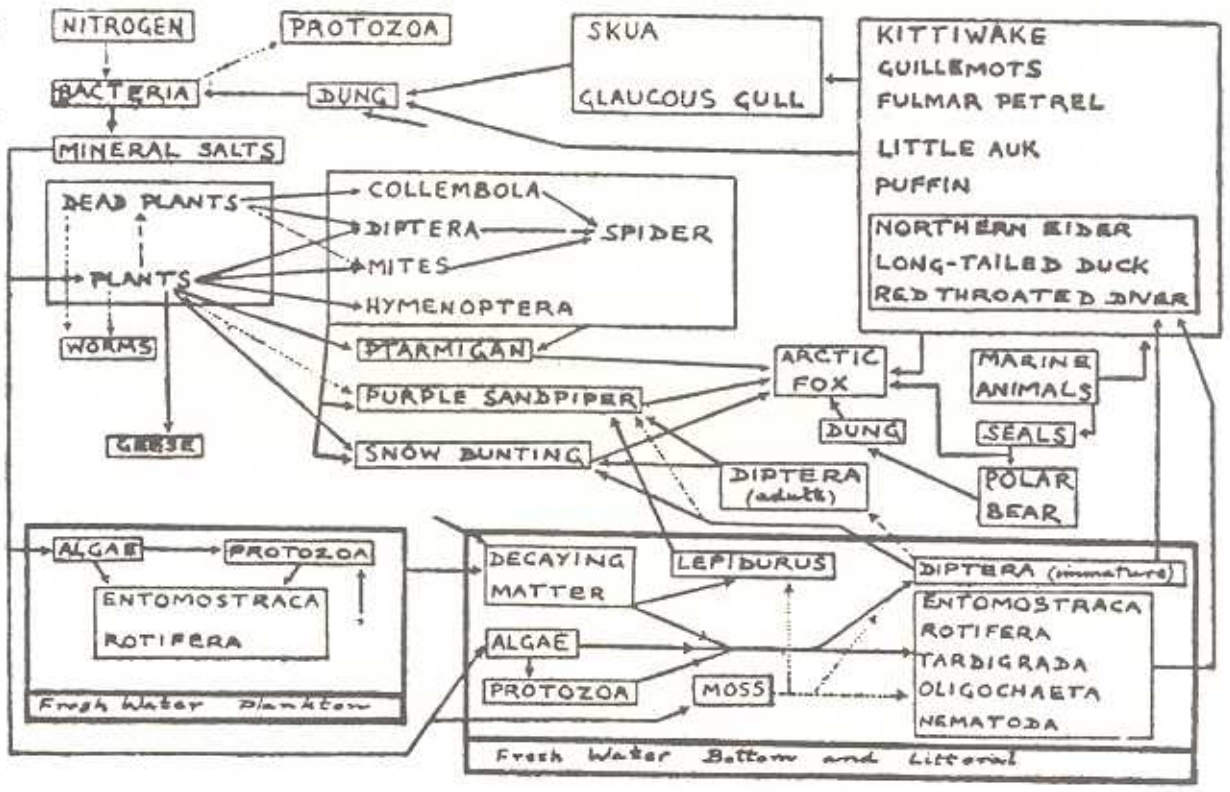


Figure 4. Food cycle of the animal community on Bear Island, near Spitsbergen (Charles Elton, *Animal Ecology*, Sidgwick and Jackson, 1927). Elton sometimes referred to this diagram as a "nitrogen cycle."



Figure 5. Evelyn Hutchinson at the Osborn Memorial Laboratory 1939 (Yale University Archives, Manuscripts and Archives, Yale University Library).



Figure 6. Sketch of Sir Arthur Tansley by Jane de Glehn, 1939 (by permission of the President and Fellows of Magdalen College, Oxford).



Figure 7.
Raymond Lindeman,
ca. 1939
(University of Minnesota Archives).

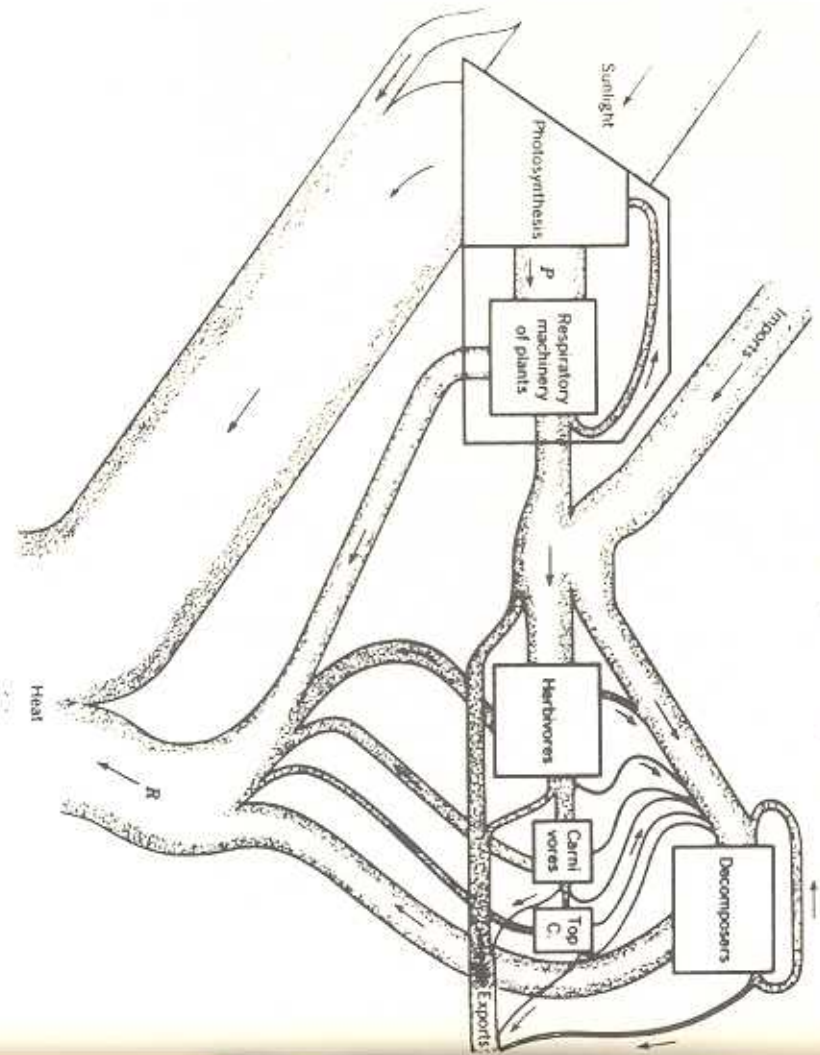


Figure 8.
Simplified diagram of energy flow through Silver Springs, Florida
(Howard T. Odum, *Environment, Power, and Society*, John Wiley,
1971).



Figure 9.
Eugene and Howard Odum receiving the 1987 Crafoord Prize. *Left to right:* Mrs. Elizabeth (H. T.) Odum, Mrs. Martha (E. P.) Odum, Howard T. Odum, Mrs. Anna-Greta Crafoord, Eugene P. Odum, King Carl XVI Gustaf (Royal Swedish Academy of Sciences).