PART 1

Foundational Papers

Defining Ecology as a Science

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The origins of ecology as a science began with the application of experimental and mathematical methods to the analysis of organism-environment relations, community structure and succession, and population dynamics. The word "oecology" was first coined in the 1860s by a German zoologist, Ernst Haeckel. As a convert to Charles Darwin's theory of evolution, Haeckel believed that a term was needed to refer to the study of the multifaceted struggle for existence that Darwin had discussed in his 1859 treatise *On the Origin of Species* (McIntosh 1985, pp. 7–8).

In his book, Darwin had reviewed the diverse meanings of the struggle for existence, a metaphor standing for all the factors that affected the organism's survival and reproduction. His argument was influenced by his reading of Thomas Robert Malthus's controversial *Essay on Population*, first published in 1798, which pointed out that populations would, if left unchecked, tend to increase geometrically and would soon outstrip their food supply. Malthus had asked his readers to consider the consequences of the struggle that would inevitably follow from this population pressure.

He concluded that because this population pressure could never be eliminated, we would never be able to create a truly utopian society where war, famine, and vice were absent. He was advising the utopian social thinkers of his time to adopt a more realistic and conservative estimate of the potential for human progress.

Darwin read the sixth edition of the *Essay on Population* (1826) in 1838, soon after returning from a five-year voyage around the world. In England, when he had had time to reflect on the observations he had made, he realized that species had probably originated from preexisting species and had not been specially created by God. Reading Malthus gave him a crucial insight that eventually led to his theory of natural selection. By turning Malthus's logic back to the natural world, Darwin deduced that the tendency to overproduction would lead to intense competition, heavy mortality, and therefore to an unconscious selection process. Given a long enough period of time one species might split into several new species, each with adaptations shaped by the selective pressures of climate, food supply, predation, and competition. Darwin described his theory as the law of Malthus

applied to the natural world, but in fact he had brilliantly reversed Malthus's conclusions by showing that the struggle for existence was the mechanism for open-ended evolutionary change.

The struggle for existence included all forms of competition, direct and indirect, between organisms. One of the most important arguments in *Origin of Species* was the emphasis Darwin placed on competition between individuals of the same species as the chief mechanism of evolutionary change. Ernst Mayr (1982) has argued that the reading of Malthus was so important because it made Darwin realize that the struggle for existence mainly occurred *within* the species, that the members of a population were competing with each other. It was common in natural history writing before Darwin to describe a struggle for existence between different species, for instance between predator and prey. Naturalists accepted the idea that predators would kill off the weak, old, or diseased members of a prey population, in other words, that predation was a form of selection of the unfit. This kind of selection, they thought, actually served to preserve the character of the prey species, because only the deviant individuals were picked off.

But competition within the population could produce real changes, as Darwin recognized. If closely similar individuals were competing intensely for resources, then those with traits that gave them superior competitive ability would eventually replace the inferior and less prolific members of the population. Therefore natural selection was a genuinely creative force, not merely a mechanism for the preservation of the species type. Competition *within* the species had quite a different significance from competition *between* species. Recognition of the intensity of competition between closely related forms was also crucial to the understanding of the subtlety of adaptation and the patterns of species' replacement over a large geographical area.

The work of Darwin and other naturalists of the late-nineteenth century stimulated a more rigorous approach to natural history. In the United States, naturalists such as Stephen Alfred Forbes (1844–1930), Henry Chandler Cowles (1869–1939), and Frederic Edward Clements (1874–1945), all working in the Midwest, began to develop new quantitative methods and theoretical principles that would eventually lay the foundations for a new science called ecology. The term "ecology" was first used in America by a group of professional botanists, who in the 1890s began openly to reject traditional descriptive methods of natural history and concentrated instead on physiological studies of the relationship between organisms and their environment (Cittadino 1980). These botanists were greatly influenced by German and Danish studies in plant geography, themselves an outgrowth of the European Darwinian tradition of research on adaptation and environment. In the creation of the discipline of ecology botanists led the way, but their zoological colleagues followed closely behind and by the 1920s had taken the lead in population studies, which became a major field of research in the 1930s.

The science of ecology, as it was understood both by botanists and zoologists at the turn of the century, signified a dynamic, experimental approach to the study of adaptation, community succession, and population interactions. For botanists in particular, the ecologist was a kind of "outdoor physiologist," someone who studied adaptation and community evolution in the field using the same rigorous methods that the physiologist employed in the laboratory. These botanists were interested in whether the evolution of species could be controlled experimentally by altering the environment, a goal that had obvious agricultural applications. Most of the early biological surveys and other ecological studies were done in connection with the agricultural experiment stations and land-grant colleges being established by the government in each state at the end of the nineteenth century. In the early-twentieth century, much ecological research on evolution, adaptation, and community succession was funded privately by the Carnegie Institution, which established a Desert Botanical Laboratory near

Tucson, Arizona in 1902. In 1904, the Carnegie Institution also opened an experimental station for studies of evolution at Cold Spring Harbor, New York, which became a center of genetics research.

As a high profile and trendy scientific field, ecology attracted many practitioners, but the standards of the new science were not always very rigorous. Hence the complaint voiced by one botanist of the old school, Charles E. Bessey, who bemoaned the popularity of this latest "fad," which seemed only to distract from serious botanical research (Cittadino 1980, p. 171). But the professional interest in ecology was also serious and the field flourished, despite heavy competition from that other great "fad" of the twentieth century, genetics. The Ecological Society of America held its first organizational meeting at the end of 1914 and was officially constituted in 1915 with 284 charter members (Burgess 1977).

Stephen Forbes, who began his ecological career in Illinois in the 1870s, was greatly influenced by Darwinian biology and by the efforts in America to raise the standards in natural history research by such eminent scientific figures as Louis Agassiz, who in 1859 founded the Museum of Comparative Zoology at Harvard University. Stimulated to pursue ecological work by the research ideals of men such as Agassiz, Darwin, and Thomas Henry Huxley, Forbes undertook detailed analyses of the food relations of insects, birds, and fish within the community, believing that exact information was needed before the value of a species to society could be assessed. The immediate justification for his research was its practical importance: his analyses of food webs were pioneering attempts to give agriculture a scientific basis (Forbes 1880). But Forbes also appreciated the importance of setting his data into the broader theoretical framework of evolutionary biology. The enormous labor involved in ecological research was justified partly by its potential contribution to general questions involving the nature of adaptation, the causes of variation, and the origin and extinction of species.

Forbes accepted Darwin's argument for evolution by natural selection, but missing from Darwin's discussion was an explanation of how the struggle for existence produced what seemed to be a well-regulated world where population densities remained fairly stable from year to year. This idea of a balance in nature was commonly accepted by natural historians well before Darwin. Forbes integrated this traditional belief, which harkened back to an earlier teleological view of nature as harmoniously regulated for the benefit of all in accordance with divine wisdom, with the new theoretical writing on evolution. To achieve this integration, he had to go beyond Darwin's own discussion, which did not really address the problem of how balance was achieved between populations.

The theoretical support for the common sense idea that nature was self-regulating came largely from Darwin's compatriot Herbert Spencer (1820–1903), a philosopher and evolutionist who coined the phrase which we now associate with Darwinian evolution, "survival of the fittest." Spencer was trained as an engineer and thought of nature as a moving equilibrium between opposing forces, in this case the forces of population increase and decrease. Spencer believed that there was a necessary adjustment of fertility to mortality, a balance that produced rhythmical population changes about a stable equilibrium value. As evolution progressed, these forces came into perfect balance; Spencer believed that eventually evolution itself would come to a halt (Kingsland 1985; Spencer 1874). Spencer's analysis of evolution, though based almost entirely on armchair reasoning rather than direct observation, was attractive to his contemporaries partly because it supported the prevalent Victorian belief in a harmonious, progressive world. Let the struggle for existence work itself out unfettered, he thought, and improvement would inevitably result (Kingsland 1988).

Spencer himself was not really a Darwinian evolutionist, though he accepted Darwin's main argument for natural selection. He believed that a more important mechanism of change was direct, hereditary adaptation to the environment.

Adaptive change in direct response to the environment was known as "neo-Lamarckian" evolution, named after the French zoologist Jean-Baptiste Lamarck, who in 1809 proposed a theory of evolution based partly on the idea that characteristics acquired during an organism's lifetime could become hereditary (Lamarck 1984). In the late-nineteenth century most evolutionists viewed both Darwinian selection theory and the neo-Lamarckian theory of direct adaptation to the environment as complementary mechanisms of evolutionary change. Spencer's writings did a great deal to popularize Lamarckian evolution. Darwin himself was more accepting of the inheritance of acquired characteristics in later editions of the *Origin,* especially when he was faced with the problem of explaining how habits evolved into hereditary instincts.

Influenced by both Darwin and Spencer, Forbes was concerned to show that despite the intensity of the struggle for existence, natural selection was a beneficial force because it tended to restore a healthy equilibrium to the community. Darwin's struggle for existence and Spencer's balance of forces combined to create an image of nature which was both benign and thrifty. By combining a Spencerian outlook with Darwin's theory of evolution, Forbes developed the theme of a "common interest" between a species and its enemies, the idea being that natural selection would adjust reproductive rates so that they balanced mortality.

His classic description of the community along these lines was put forth in his essay of 1887, "The Lake as a Microcosm," which set out the main goal of ecological research: to analyze how harmony is maintained through the complex predatory and competitive relations of the community. By using the metaphorical language of the "sensibility" of the organic complex, the essay drew attention to the way all species were bound up with others within the community. This concept of the ecological community had European precedents. Karl Möbius's pioneering study of oyster culture had been published in America in English translation in 1883. In this essay Möbius had proposed

the term "biocoenosis" for a community of species inhabiting a definite territory (Möbius 1883). Forbes's discussion developed the concept of the community in more detail and his essay exemplifies the ecological viewpoint at that time. His assumption of balance between reproduction and mortality was remarkably long-lived in the ecological literature. As late as the 1950s David Lack had occasion to criticize this still-prevalent assumption; he proposed instead that the reproductive rate in birds was adjusted not to mortality but to the food supply available to the young (Lack 1954).

While animal ecologists focused on community structure and population dynamics, plant ecologists concentrated on ecological succession. Henry Chandler Cowles, whose research concentrated on the sand dunes in the Chicago region, developed a dynamic perspective which he called physiographic ecology (Engel 1983). Trained as a geologist, Cowles stressed the constant dynamic interaction between plant formations and the underlying geological formations. The physiographic viewpoint saw the flora of a landscape as an ever-changing panorama; the ecologist had to discover the laws governing these changes. Cowles's studies of the Indiana dunes yielded the first thorough working out of a complete successional series. Cowles was able to accomplish this task by assuming that vegetational changes in space paralleled successional changes in time. Therefore, as one walked inland from Lake Michigan, one also walked backwards in time. By putting together the spatial sequences of plant formations, Cowles reconstructed the temporal development of plant associations (Cowles 1899). We have included here excerpts from his first major study of the dunes, published in 1899, which illustrates his view of ecology as a study of process. The references accompanying his article reveal the important precedents in European ecological research that served as a foundation for the American school.

Cowles's account of succession was never dogmatic. Though he believed that succession tended toward a stable equilibrium, he did not believe that this equilibrium state was ever

reached. Moreover, successional stages leading to the climax community—the final stage of succession—were never in a straight line, but could even regress in the normal course of events. His concept of the community included not only the idea of a continuous, never-ending process of change, but also the idea that all the organisms were connected in a vast, complicated symbiosis.

While Cowles was tracking the ever-shifting landscape of the dunes, his colleague Frederic Clements was studying the more stable grasslands and conifer forests of the western prairie. He developed a theory of the plant community that differed in significant ways from that of Cowles (Tobey 1981). Clements was important also for publishing the first American textbook in ecology, *Research Methods in Ecology* (1905), which discussed the statistical and graphical analytical methods he and other Nebraskan ecologists developed from 1897 to 1905. His ecological theory rested on two ideas, the concept of ecological succession of plant formations, and the treatment of the plant community as a "complex organism" undergoing a life cycle and evolutionary history analogous to the individual organism. The formal presentation of his theory appeared in 1916 in his monumental study *Plant Succession.*

Clements was also influenced by Herbert Spencer and believed that organisms evolved by direct adaptation to changes in the environment. In America the neo-Lamarckian school was prominent during the 1890s, the decade when Clements was developing his ideas (Bowler 1983). He held fast to his Lamarckian ideas, even believing that body cells could modify the germ plasm, long after the theory had been roundly challenged and mostly discredited in America by the 1920s. In Clements's theory, the plant community could be analyzed as a complex organism which grew, matured, and died like an individual organism. Following the Lamarckian model of evolutionary change, the process of plant succession entailed a continual interaction between the habitat and the life forms of the community. The habitat and the populations acted upon one another in a recip-

rocal way, until finally a stable state, the climax, was reached. If the climate remained stable and no humans intervened, the climax might persist for millions of years.

Clements believed that one of the important processes directing succession was competition between similar plants (Clements, Weaver, and Hanson 1929). Species of trees, for instance, were described as competing sharply when together, whereas the relation of shrubs to trees was thought to be one of subordination and dominance rather than competition. Clements thought that the process of succession reduced the amount of competition within the community as a whole by setting up stable dominance hierarchies among the species of the community as it moved toward the climax stage. The overall character of the climax formation was defined by its dominant plant forms. Though Clements did come to appreciate the importance of animal populations in succession, largely through his collaboration with Victor Shelford, a leading animal ecologist and former student of Cowles's, he continued to think of the community as structured mainly by its plant formations.

Clements also used the idea of the climax to develop a system of classification for the units of vegetation. He subdivided the units of the climax formation into various categories with parallel categories of successional change. His use of esoteric Greek and Latin terms, a penchant that others found tedious, as well as his emphasis on quantitative methods reveal his desire to build ecology into a rigorous discipline. His classification system and theoretical framework dominated American plant ecology in the first decades of the twentieth century.

Clementsian doctrine did not go unchallenged (McIntosh 1985, pp. 76–85). On the agricultural front, wheat farmers in the midwestern prairie criticized the climax theory largely because it advocated a more cautious use of these marginal lands and therefore threatened their livelihood (Worster 1979). The creation of the Dust Bowl in the 1930s, however, showed the wisdom of the kind of ecological awareness that Clements had advocated.

But Clements's fellow ecologists also criticized aspects of his theory. British ecologist Arthur G. Tansley disagreed with the organismic metaphor, though he defended Clements's idea of the plant formation as a natural unit. He preferred to call the community a "quasi-organism" and in 1935 coined the word "ecosystem" as a more accurate characterization of the vegetational unit (Tansley 1935; Tobey 1981). The shift from a biological to a physical model for ecology also opened the way to a mathematical analysis of the system. Fittingly, the volume of *Ecology* in which Tansley's 1935 critique appeared was dedicated to Cowles, who also had no use for the organismic metaphor. Forrest Shreve, an ecologist at the Desert Laboratory of the Carnegie Institution, with which Clements was also affiliated, criticized the idea of the climax as a stable formation controlled by the environment.

These arguments were echoed by another critic, Henry Allen Gleason (1882–1975), who proposed an "Individualistic" concept of the plant association in place of the organismic metaphor (McIntosh 1977). Gleason argued that fixed and definite vegetational structures did not exist. To be sure, it was possible to identify communities that were uniform and fairly stable over a given region, but he denied that all vegetation could be segregated into such communities. He was very conscious of the way that short-term environmental changes in time and space could have profound effects on the abundance of species in an area. Taking the opposite view from Clements, Gleason argued that every plant association was the unique product of the fluctuating environmental conditions of a particular time and place. It was not meaningful, in his view, to compare the plant community to an organism, nor was it possible to create a precisely logical classification of communities, as Clements had tried to do.

These criticisms did not persuade Clements to drop the organismic metaphor or to change his classification system in any way. The only major change in Clements's ideas in later years was to recognize the existence of animal populations as an integral part of the community.

However, by the 1950s plant ecologists had abandoned many of the central principles of Clementsian dogma, as well as the more cumbersome features of his classification system, as inappropriate or unproductive. Instead of the "complex-organism" analogy, postwar ecology emphasized the functional system formed by community and environment, the ecosystem (Whittaker 1977).

In the 1920s, animal ecologists who were analyzing community structure began to develop the concept of the ecological niche. Charles Elton's text of 1927, *Animal Ecology*, which is still an excellent introduction to the subject for students, defined the niche concept in the context of his discussion of the food chain (Elton 1966). Before Elton, the niche was a nontechnical term referring to an abstract space in the environment which could be full or empty. Elton employed the idea of the niche, meaning an animal's "place," to redirect attention to the food relationships within the community. He believed that ecologists had to pay more attention to what the animal was actually doing in the community. He used the term niche to refer to the animal's place in the food chain, which also defined the animal's economic role in the community. Elton considered the niche to be a smaller subdivision of the traditional groupings of herbivore, carnivore, insectivore, and so on. By studying how different species occupied the niches within the community, that is, how they took on the major economic roles in the food cycle, one could perceive the basic similarity in structure between communities that appeared quite different in their species composition.

As a general economic category, therefore, a single niche could be occupied by different species. Elton's discussion of the niche did not include what we now call "the competitive exclusion principle," or the principle that two different species cannot occupy the same niche (Hardin 1960). Even before the term niche was used to designate the organism's habitat, this basic principle was well known to naturalists in the nineteenth century. Stephen Forbes, for instance, described in 1884 how species of insects feeding on the strawberry plant avoided direct

competition by feeding at different times (Winsor 1972). One of the central problems that field naturalists studied in the early twentieth century was the coexistence of closely allied species and the ways that similar species evaded competition.

Joseph Grinnell (1877–1939), an expert on North American birds and mammals, connected the idea of competitive exclusion to the term *niche* in 1917 when he asserted that "no two species regularly established in a single fauna have precisely the same niche relationships." In his usage the niche was roughly synonymous with habitat. As a natural historian in the twentieth century, Grinnell was part of a shrinking population of field naturalists who published descriptive rather than experimental studies (Hutchinson 1978, pp. 152–54). Descriptive field studies of this kind were often disparaged by experimental biologists who wanted to establish the experimental approach to evolutionary biology as the more rigorous method. But Grinnell's brilliant research in natural history was recognized by contemporary naturalists who resisted the increasing specialization of biology. We have included here the article in which Grinnell refers to competitive exclusion as an axiomatic principle.

Elton also recognized the essential idea of competitive exclusion. Elsewhere he used the term niche in its older meaning of habitat rather than of a position in the food chain, and in that context he adopted Grinnell's conclusion that the limited number of niches and competitive exclusion determined the number of species in an association (Elton 1933, p. 28). But Elton did not raise the principle of competitive exclusion to the status of a key organizing idea of ecological theory. The competitive exclusion principle framed in terms of the niche concept became a more central and much debated ecological idea following the work of a young Russian ecologist, Georgii F. Gause (1910–1986), who designed his doctoral dissertation around an experimental analysis of predatory and competitive interactions between species of yeast and protozoa. These results appeared in 1935 as a small book called *The Struggle for Existence*. Unlike

Elton's discussion of community structure, Gause's analysis made use of new mathematical modeling techniques that were being developed in American and European ecology in the 1920s. In fact, his book drew many ecologists' attention to this mathematical work for the first time.

The starting point for mathematical ecology was the analysis of population growth within a single species. Raymond Pearl, a statistician studying human population change after the First World War, discovered in 1920 that human population growth over time seemed to follow a regular, S-shaped curve which he called the "logistic curve" (Pearl and Reed 1920). The differential equation of the curve was $dN/dt = rN (K - N)/K$, where N represents the number of individuals, t the time, r the maximum rate of increase of the population, and K the upper limit of population growth. In the course of his research, Pearl also discovered that a Belgian mathematician named Pierre-François Verhulst had analyzed the curve nearly a century earlier, as part of a larger attempt to determine the law of population growth. The term "logistic" was Verhulst's term. This research had been entirely forgotten until Pearl resurrected it (Kingsland 1985). Determined not to suffer Verhulst's fate, Pearl made strenuous efforts to publicize his discovery of this curve, which (unlike Verhulst) he regarded as an actual law of population growth, comparable to Boyle's law in chemistry. Pearl was responsible for having Gause's book published by an American publisher, no doubt realizing that it would also help to advance his own reputation through Gause's application of the logistic curve to ecological theory.

Pearl's claims were controversial. He carried on an active debate about population growth with social scientists and biologists throughout the 1920s and 1930s. All of this discussion generated a large literature that helped to publicize the curve. Most of Pearl's opponents agreed that although Pearl was incorrect to regard the curve as a law of growth, it was a convenient description of growth because the equation describing it was easy to derive by verbal logic and easy to translate into biological terms. As such,

it came to be used by ecologists in the 1930s who wanted to study population fluctuations mathematically. Fisheries ecologists in particular used and developed mathematical models based on the logistic equation (Cushing 1975).

The logistic equation had also been used independently by Italian physicist Vito Volterra (1860–1940) to construct a basic model of competition between two species (Kingsland 1985). Volterra had become interested in ecological problems in the 1920s when his daughter's fiance asked him to analyze certain changes in fish populations in the Adriatic during and after the First World War. Intrigued by the possibility of creating a mathematical science of the "struggle for existence," Volterra took up this challenge and devoted roughly fifteen years to exploring mathematical ecology. His formulations were so technical that they were beyond the reach of most ecologists; even today only his simpler models are well known. Apart from a model of competition, he also developed a model of predation in a two-species system, which coincidentally had been anticipated by Alfred James Lotka (1880–1949), an American mathematician and demographer. The two-species model of predation is now known as the "Lotka-Volterra equations" and is the starting point for most modern discussions of predation.

In 1925 Lotka published an unusual treatise which included a mathematical study of energy transformations within the biosphere, forming the basis for a new science which he called "physical biology" (Lotka 1925). Lotka, trained as a physical chemist, hit on the idea that one could apply thermodynamic principles to biology along the lines of physical chemistry in order to create a new science that focused on energy transformations within the biosphere. Over twenty years later his ideas on the subject were gathered into the book *Elements of Physical Biology*. Though he was not an ecologist, his wide-ranging discussion touched on many ecological problems, including such topics as food webs, the water cycle, and the carbon dioxide, nitrogen, and phosphorus cycles. Lotka's efforts to analyze the earth as a single undivided

system, a kind of giant engine or energy transformer, were unprecedented in ecological theory, although his book coincided with a similar biogeochemical approach to ecology advanced in the 1920s by Vladimir I. Vernadsky in Russia. Lotka's clear exposition of the systems approach later influenced Eugene P. Odum and Howard T. Odum, who developed ecosystem ecology in the 1950s.

Lotka's desire to make his new science mathematical led him into the study of population growth and predator-prey interactions. His demographic analysis of stable populations influenced Patrick H. Leslie, who developed a method of analyzing populations using matrix algebra in the 1940s. Lotka was the first to explore the analysis of population interactions using sets of simultaneous differential equations, a method similar to Ludwig von Bertalanffy's "general system theory" of the 1950s, though Bertalanffy did not give Lotka credit for his prior work. As far as population dynamics were concerned, Lotka was not especially interested in competition; the mathematical analysis of competitive interactions was therefore carried forward mainly by Volterra.

Gause had read the publications of Pearl, Lotka, and Volterra and decided to test some of these simple models in a laboratory setting. In his book he referred to the principle of competitive exclusion in passing, regarding it as a natural extension of previous work and not worthy of special attention. A second and more sophisticated series of experiments was published in 1935 in a French monograph that unfortunately was not well known to ecologists (Gause 1935). In this second monograph he developed the idea that competition would force two species into separate ecological niches, thereby enabling them to coexist in the confined space of the test-tube environment.

Subsequent fieldwork on ecological succession that buttressed his laboratory experiments led Gause to appreciate the idea that competitive exclusion was the key to the structure of whole communities (Gause 1936, 1937). He began to think of the niche as a unit structure over which species fought for possession; each spe-

cies' niche was the place where it alone enjoyed full advantage as a competitor. This meant that at the basis of the structure of the community lay the niche structure and that the stable, regulated community was actually a result of the competition between similar species. The principle of competitive exclusion therefore provided a way of relating community structure and the process of succession directly to the ongoing competitive interactions between the populations within the community. This explanation of community succession was compatible with Clements's ideas about competition, though Gause rejected the organismic metaphor as superfluous. In 1939 he asserted the centrality of the competitive exclusion principle in a commentary to a review of population ecology by Thomas Park (1939).

Gause's historical importance is not that he invented a new principle, but that he drew attention to what had been considered an axiomatic principle by making it a focus of the ecological theory of community structure. As soon as competitive exclusion began to be used as a central organizing idea, it generated controversy mainly because of the structure of the argument. Critics suggested that the principle was tautological and therefore was not useful because all it really told us was that no two species have identical requirements, which is true but trivial. We do not know the nature of these ecological requirements in advance, however. The principle focuses our attention on the fact that species must find ways to partition limited resources in order to coexist. We can discover how they do this by looking for cases where the principle seems not to apply and asking how species manage to live together. What we find most often is that the species have partitioned their resources in subtler ways than we had suspected. Therefore, the principle of competitive exclusion is useful in steering us toward a more profound analysis of ecological relationships. David L. Lack, G. Evelyn Hutchinson, and Robert H. MacArthur developed Gause's hypothesis along these lines in their studies of competition. In the 1960s studies of competition and the niche grew into major fields of research

in evolutionary ecology, despite continuous controversy over the meaning of competition and the difficulty of measuring competitive interactions in the field.

A rather different approach to competition, population regulation and mathematical modeling was advanced by Alexander John Nicholson (1895–1965), an Australian entomologist, who teamed up with Victor Albert Bailey, a physicist, in a theoretical analysis of host-parasite interactions. Nicholson devised the original arguments behind the models and Bailey converted them into mathematical form. Reasoning by physical analogy, Bailey considered the movement of parasites in search of hosts to be analogous to Maxwell's theory of the mean free path of a particle in a gas. He assumed that density was uniform and that search proceeded randomly in the population as a whole. Volterra had used a similar analogy in his own models, but where Volterra and Lotka both used continuous-time models, Bailey used more realistic discrete-time models.

Nicholson and Bailey tried to improve on the Lotka-Volterra predation model by taking into account the effects of competition from members of the same species, as well as delays caused by the age distribution of the populations. Nicholson believed that any factor controlling populations had to act with increasing severity as density increased (Nicholson 1933). Only competition seemed to fulfill this requirement; therefore, he considered competition the chief mechanism of population regulation. In their models, Nicholson and Bailey tried to take into account the competition occurring when animals were engaged in a search for essential resources, though they could not directly measure the effects of such competition. With these and other adjustments, they found that instead of the steady-state oscillations of the Lotka-Volterra model, their models predicted an unstable system of increasing oscillations in their theoretical populations. In general, they hoped for a more exact treatment of population regulation with more detailed consideration of the alternative outcomes that would result from making different biological assumptions. The

article which we have excerpted here was intended to be the first part in a series on population regulation, as indicated in the title, but the other parts were never completed. Harry S. Smith and Paul DeBach published some of the first experiments based on Nicholson's work in 1941 (DeBach and Smith 1941), and George Varley published the first field test of Nicholson's predictions in 1947 (Varley 1947). David Lack (1954) was also influenced by Nicholson's arguments. The question of density-dependent versus density-independent population regulation erupted in controversy in the 1950s and 1960s, with the main opposition to Nicholson's ideas and to mathematical approaches in general being voiced by H. G. Andrewartha and L. C. Birch (Andrewartha and Birch 1954).

With all the mathematical modeling of the 1930s, there was almost no attempt to incorporate population genetics into ecological models. Just as population geneticists tended to assume that the environment was constant, population ecologists assumed that their populations were genetically uniform. Although ecologists were aware of the mathematical work of J. B. S. Haldane, R. A. Fisher, and Sewall Wright in the 1920s and 1930s, there was little overlap between ecology and genetics until the 1960s. Two notable exceptions in these early decades were E. B. Ford at Oxford University, who collaborated with R. A. Fisher and developed ecological genetics starting in the late 1920s (Ford 1980), and V. A. Kostitzin, a Russian geophysicist living in Paris in the 1930s, who combined the Lotka-Volterra model with an evolutionary, genetic perspective (Scudo and Ziegler 1978). Kostitzin's work, which ended during the Second World War, has made virtually no impact on ecology.

While the new methods and concepts of population ecology were being brought to bear on problems of community structure and succession, another young ecologist, Raymond Lindeman (1915–1942) tackled the problems of succession from a physiological perspective. He fashioned a synthesis of physiological ecology and community ecology which he called

the "trophic-dynamic aspect" of ecology. The 1942 article that set out this viewpoint was part of a series of articles on the ecology of a senescent lake, Cedar Creek Bog in Minnesota, which was the subject of his doctoral dissertation. This final article, published posthumously, was path-breaking in its general analysis of ecological succession in terms of energy flow through the ecosystem.

The trophic-dynamic viewpoint was an attempt to demonstrate how the day-to-day processes within a lake affected the long-term changes of ecological succession. From our perspective, using short-term cumulative changes to explain long-term dynamical changes may seem obvious, but ecology had tended to develop along two separate paths that made this kind of integrated analysis difficult. One branch of ecology, termed *autecology*, focused on physiological relations between organisms and environment, while the other branch, termed *synecology*, mapped out the long-term patterns of community succession. Both branches dealt in different time scales and focused on different sets of problems appropriate to the different time scales. Lindeman brought them together again.

Instead of looking at competitive interactions, as Gause had done, Lindeman focused on the trophic or nutritional relationships within the lake. His decision to group the inhabitants of the lake according to their position in the food cycle was stimulated by the work of Charles Elton, who was the first to describe the relationship between food habits and community structure. Lindeman found that there were two parallel food cycles operating in the lake which merged in their common link with bacterial decomposers. While studying the cycling of nutrients through the lake, it became clear to Lindeman that any attempt to separate the organisms from their abiotic habitat was highly artificial. Instead, the lake was an integrated system of the biotic and the abiotic, to which he gave the name "ecosystem." The remaining problem was to understand how all of the processes involving the influx of nutrients and

removal of nutrients from the lake, acting in combination with the food cycle, could affect the rate of succession of the whole ecosystem.

Lindeman's mature analysis of the problem was worked out in 1941 while he was visiting G. Evelyn Hutchinson at Yale University. In a 1940 article Hutchinson and A. Wollack discussed the relationship between trophic processes and succession. In a footnote they called attention to the limnological method, as epitomized by American ecologists Edward A. Birge and Chancey Juday, of isolating a suitable volume of space, such as a lake, and studying the transfers of matter and energy across the boundaries of this volume (Hutchinson and Wollack 1940). This approach, though useful for its emphasis on physical and chemical processes, treated the lake as a "black box" without the detailed mapping of the trophic structure that Lindeman was attempting. In a major treatise on biogeochemical processes that was still in progress while Lindeman was visiting Yale, Hutchinson had independently begun to think of classifying biological formations and their developmental stages in terms of photosynthetic and consumer group efficiencies. With access to Hutchinson's research and lecture notes, Lindeman developed a theory of successional change which emphasized the ecological efficiency of energy transfer over the long term (Cook 1977).

One idea that Hutchinson himself did not use greatly, but which Lindeman made the centerpiece of his study, was the ecosystem concept. Though Arthur Tansley had introduced the term in 1935 to describe the climax community, his use of the ecosystem concept had little impact on ecology. By reviving the concept in the context of a dynamic analysis of succession, Lindeman showed how it could be used to organize ecological ideas. The ecosystem unit was a significant departure from traditional interpretations of succession. Frederic Clements and Victor Shelford had organized their 1939 text *Bio-Ecology* around the unit of the plant-animal formation, known as the biome. Their discussion of change within the biome drew on the complex-organism analogy, so that succession was the result of the reciprocal interaction between the living community (biome) and its habitat, moving through stages comparable to the developmental stages of the individual organism (Clements and Shelford 1939).

German limnologist August Thienemann (1918, 1926) had also discussed the relationship between the community (known in Europe as the *biocoenosis*) and the habitat (or biotype) in the context of succession. His work was important for showing that the union of community and habitat need not result in a static, perfectly cycling system. However, he also used an organismic analogy, with succession being the product of the reciprocal interactions between "biocoenosis" and "biotype." By 1939, he combined the biocoenosis with the biotype to form a higher unity called the "biosystem" (Thienemann 1939). His approach differed from Lindeman's in lacking any attempt to work out precisely the relationship between the development of the unit and the internal trophic processes of the system.

It is interesting to note that when Lindeman sent his essay to *Ecology* for publication, two eminent limnologists, Chancey Juday and Paul Welch, recommended that it not be published, largely because it was too theoretical and went far beyond the data available at the time (Cook 1977). Welch recommended that Lindeman set the manuscript aside for ten years in the hope of accumulating a better data base. With Hutchinson's strong support of the manuscript, the editor of the journal, Thomas Park, decided to publish a revised manuscript despite the negative reviews. In fact, Lindeman never saw the article in print because he died in 1942 after a long illness; he was twenty-seven years old. Though published without the desired supporting data, his article opened up new directions for the analysis of the functioning of ecosystems.

These are some of the major publications in ecology which formed the basis for a continuing research tradition in community studies, succession, ecosystem analysis, population

dynamics, and organism-environment relations. Many of the ideas and methods presented in these papers were controversial, especially the complex-organism analogy and the use of mathematical techniques for modeling population interactions. Mathematical modeling was controversial because it seemed oversimplified and generated conclusions that went beyond the available data. Many of the laboratory studies that grew from these theoretical forays were criticized for being inapplicable to the more complex field environment, while many field studies were in turn criticized for being too descriptive or not being related to theoretical principles. Ecology is such a heterogeneous science that arguments about methods, approaches, and definitions of central terms are nearly impossible to avoid. In the following sections we consider in detail the elaborations of ecological science that stemmed from these sometimes crude but often imaginative and optimistic beginnings.

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