An Entangled Bank

The Origins of Ecosystem Ecology

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To
NORM FORD and PAUL FARBER,
Teachers and Friends

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An Entangled Bank

Battle within battle must ever be recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains uniform for long periods of time.

—Charles Darwin, *On the Origin of Species*

Charles Darwin presented an ambiguous picture of nature in his greatest work, *On the Origin of Species*. Nature was a battlefield on which individuals ceaselessly struggled in the "war of nature," but it was also a stable complex of interacting parts. Indeed, a recurring theme in the book is the "entangled bank" covered with diverse plants and animals interacting according to definite laws of nature similar to those governing the movement of the planets.[1] Darwin marveled at nature's "web of complex relations." Take for example, the close interactions among flowering plants, humble-bees, mice, and cats near Down House. According to Darwin, experience showed that red clover almost totally depended upon humble-bees for pollination; other bees did not visit the clover because they could not reach the nectar in the narrow, tubular flowers. The population of humble-bees was regulated by field mice that destroyed the bees' nests. The number of mice depended on the number of cats in the neighborhood. Thus, Darwin concluded, the population of clover might well depend indirectly on the population of cats.[2]

Darwin's example provides an excellent illustration of basic ecological principles. Species do not exist completely independently, but they often form interacting groups. Regulation of one population by another may be indirect. Sometimes a single species may have a pervasive influence on several other members of the web. For the modern reader all this is immediately obvious in Darwin's writing. Yet despite his confidence that the struggle for existence could explain natural order, Darwin did not rigorously do so in 1859. His discussions of nature's "entangled bank" were short, literary passages interspersed in his more technical discussion of speciation and the evolution of adaptations. Only during the twentieth century did biologists propose general theories to explain the type of observations that Darwin made near Down House. This became the intellectual domain of community and ecosystem ecology.

Darwin's two views of the living world—machinelike stability and chaotic warfare—appear anomalous. But were they? Historians disagree on this matter. In his history of ecological ideas, *Nature's Economy,* Donald Worster emphasizes the inherent contradiction between these two views.[3] In fact, he claims that this intellectual dichotomy reflected a fundamental division in Darwin's psyche. His pastoral existence at Down House and the competitive professional life of London represented psychological poles analogous to the entangled bank and the battlefield of nature. Both intellectually and psychologically he struggled with these polarities, but in the end they remained unreconciled. According to Worster, Darwin may have been a reluctant revolutionary, trying to temporize the idea of the struggle for existence, but violent encounter remained the dominant theme in both his evolutionary writings and psychological character.[4]

Quite a different interpretation is presented by Edward Manier. According to Manier, Darwin's concept of struggle for existence was a deliberate choice, a compromise between Thomas Hobbes's war of nature and Charles Lyell's idea of nature in a steady-state.[5] For Darwin, the struggle for existence was an extremely flexible concept that included not only face-to-face competition, but also differential reproduction, parasitism, mutualism, and adaptation to the physical environment.[6] The indeterminacy implied by natural selection fit somewhat uncomfortably with the Newtonian clockwork universe so central to the Victorian world view, and, in the end, evolution proved profoundly subversive to Victorian beliefs in stability, natural order, and progress.[7] But this was not obvious even to Darwin, who, though tending toward a view of natural laws as statistical summaries of phenomena, never completely broke with the more traditional notion of deterministic laws of nature.[8]

Several prominent ecologists have recently argued for a historical interpretation curiously similar to Worster's, with its emphasis upon the contradictory character of Darwin's composite view of nature.[9] These ecologists, all critics of the idea that nature is in equilibrium, have drawn sharp distinctions between determinism and indeterminism, stability and instability, stasis and change. These dichotomies, so it is claimed, reflect antithetical intellectual positions deeply rooted in different cultural matrices. Historically, these ecologists contend, their discipline is grounded in a dogmatic commitment to the idea that nature is in equilibrium; only recently have ecologists recognized that the living world is characterized by pervasive disturbance and instability.

Whatever scientific merits nonequilibrium ecology may have, the historical claims of its proponents can be challenged on two grounds. First, like Darwin, other nineteenth-century proto-ecologists sought an intermediate position, one that could account for both stability and instability in the natural world. Second, it appears that the transition from the Victorian clockwork universe to a more indeterminate world of instability and change produced a creative tension in biology. Far from dogmatic adherence to naive notions of equilibrium, late nineteenth-century biologists forged a set of flexible concepts for dealing with the evolutionary complexities of the natural world. These concepts were inherited by ecologists when the new discipline began to form during the early decades of the twentieth century.

The Social Organism

Although Darwin's work remained largely within the conceptual framework of nineteenth-century natural history, natural selection suggested strikingly new ways of looking at life, in general. For example, in an essay review of Ernst Haeckel's *The Natural History of Creation,* Thomas Henry Huxley speculated that natural selection might be extended into the realm of physiology. According to Huxley,

> It is a probable hypothesis, that what the world is to organisms in general, each organism is to the molecules of which it is composed. Multitudes of these, having diverse tendencies, are competing with one another for opportunity to exist and multiply; and the organism, as a whole, is as much the product of the molecules which are victorious as the Fauna, or Flora, of a country is the product of the victorious organic beings in it.[10]

Physiologically, Huxley believed, both heredity and adaptation could be explained in terms of the differential multiplication and survival of organic molecules.

Viewing an individual organism, or even a cell, as a kind of population, community, or ecosystem composed of interacting microscopic parts is an old and amazingly resilient idea.[11] During the late nineteenth century, Huxley was not the only one to envision the struggle for existence occurring within the apparently stable, multicellular organism. An even broader claim was made by Herbert Spencer. Although Huxley extended the notion of natural selection to the microcosm of the individual organism, Spencer's evolutionary philosophy employed the struggle for existence as a general law of nature acting at all levels of organization. For example, in his early essay, "The Social Organism," Spencer applied the struggle for existence to both the physiological microcosm and the social macrocosm.[12] As the title of the essay suggests, Spencer saw a close parallel between the physiological body and the body politic.

Despite the fact that Spencer's 1860 essay dealt specifically with human societies, it is particularly important to consider within the context of the history of ecology. The essay is perhaps the clearest and certainly the most concise statement of Spencer's organic analogy, a concept that was borrowed by a diverse group of late nineteenth- and early twentieth-century intellectuals. Historians have disagreed sharply over the extent of Spencer's influence, particularly in America. But, even those historians who have challenged the popular portrait of Spencer as a kind of late nineteenth-century American folk hero have acknowledged that his ideas, though often misunderstood and frequently modified, had a significant impact on American social thought.[13] Historians of biology have argued that directly or indirectly Spencer influenced the first generation of American ecologists.[14] Specifically, the idea that a group of plants and animals, or biological community, can be thought of as a kind of organism became an important element in the conceptual framework of ecology.

Spencer's programmatic goal was to explain society in biological, and ultimately physical, terms.[15] What emerged from "The Social Organism" was a mechanical/organic model that, although somewhat incongruous, was widely copied by later thinkers. Unlike many later thinkers, however, Spencer quite carefully defined exactly what he meant by "organism." For Spencer, organic entities, whether individual organisms or human societies, shared a number of distinguishing characteristics. An organism increased its mass through an orderly process of *growth.* Unlike the type of growth characteristic of nonorganismal objects such as crystals, organic growth entailed *differentiation,* an increase in complexity and division of labor. Finally, organisms exhibited important *part/whole relationships.* The parts of an organism

were interdependent; ultimately the operation of a single part of the organism depended upon the smooth operation of other parts. The whole organism had a more prolonged life than had its parts. The organism persisted as several generations of individual parts arose, grew, did their work, reproduced, and died.

Spencer was also careful to discuss possible differences between individual organisms and social organisms. For example, critics might argue that while individual organisms have definite boundaries, societies rarely have a well-defined external form. But this was only a problem if one compared societies to higher animals; if one were to consider lower plants and animals, Spencer argued, one would find the same indefinite boundaries encountered in human societies. However, Spencer considered one difference between individual organisms and social organisms critical. Although physiologically one could speak of the parts of an individual organism being subordinate to the whole, Spencer's commitment to laissez faire precluded such a relationship in human society. In society the welfare of the individual could never be sacrificed for the welfare of the whole. This difference apparently was not sufficiently troubling for Spencer to reject the organic analogy, but some others did consider it a serious problem.

Spencer's organic analogy provided later intellectuals with concepts and a language for discussing social groups in terms of development, part/whole relationships, interdependence, and integration. But the essay illustrated some inherent problems with comparing communities—whether human or biological—with organisms. Indeed, the very brevity of the essay highlighted the inconsistencies in Spencer's thought. A glaring weakness in Spencer's argument is the rather naive anthropomorphism of his organic analogy. Ironically, he himself was aware of this problem. Early in the essay Spencer criticized Plato and Hobbes for drawing analogies between social structures and organs in the human body: "Both thinkers assume that the organization of a society is comparable, not simply to the organization of a living body in general, but to the organization of the human body in particular. There is no warrant whatever for assuming this."[16] However, his conviction that both social and biological evolution followed a progressive, linear path from simple to complex, undermined this cautionary note, and Spencer proceeded to draw parallels between Victorian society, the apex of social evolution, and the vertebrate (if not the human) body. Using the type of mechanical-organic images commonly employed by Victorian writers, Spencer compared telegraph lines to nerves, railroad systems to arteries, and currency to red blood cells.[17] This tendency to equate social groups not just with some type of organism, but specifically with the highly integrated vertebrate organism has been an inherent problem with the organic analogy. During the twentieth century, biologists—both adherents and critics of the analogy—have all too willingly assumed that if biological communities or ecosystems are like organisms, then perforce they must have structures analogous to nervous systems or endocrine glands.[18]

A deeper problem in Spencer's essay, and one shared with Darwin's "entangled bank" passage, is the ambiguous relationship between competition and social stability. Although Spencer supported the socioeconomic status quo, the social theory that he advocated was, as Sidney Fine suggested, "but one step removed from anarchism."[19] Written early in his career, "The Social Organism" reflects Spencer's optimism that unregulated competition produces social stability. Elaborating on the struggle-of-the-parts theme discussed earlier, Spencer compared competition in society to the physiological competition that supposedly occurred within the body. According to Spencer, "different parts of the social organism, like the different parts of an individual organism, compete for nutriment; and severally obtain more or less of it according as they are discharging more or less duty."[20] Just as during exercise blood is diverted from digestive organs to muscles, Spencer believed that certain economic activities such as railroad expansion would temporarily divert capital from other less active industries. For the individual human within society such competition might lead to bankruptcy, and for the individual parts of the body competition might lead to atrophy; but the social consequences of competition, in both cases, were stability and progress.

It is ironic that Spencer used the expansion of railroads to demonstrate how laissez faire leads to social stability and progress. In the United States, where Spencer was so widely admired, the expansion of railroads during the post–Civil War era resulted in social strife and contributed to the economic depression of 1873–1878.[21] Contrary to Spencer's vision of unregulated competition among independent individuals, this expansion eventually resulted in the growth of industrial and governmental bureaucracy. Fearing bankruptcy, both railroad managers and investors sought to minimize ruinous competition and increasingly turned to consolidation, integration, and cooperation.[22]

The ambiguity of portraying the well-regulated social organism as a state of unregulated competition was not lost on Spencer's critics. Huxley, who had no difficulty accepting competition among molecules in the body, balked at Spencer's attempt to explain social stability in the organic body politic in terms of laissez faire.[23] The organic analogy could not be used to justify unregulated competition among individuals in society, Huxley argued, "if the analogy of the body politic with the body physiological counts for anything, it seems to me to be in favour of a much larger amount of governmental interference than exists at present."[24]

For this reason, Huxley was not particularly drawn to Spencer's organic analogy, but a diverse group of philosophers, political scientists, sociologists, and historians later embraced both the organic analogy and the belief that this analogy justified a greater regulatory role for government. For example, the historian and social critic Charles Beard, whose work exemplified the newer form of cultural organicism so influential by the end of the century, cited both Darwin and Spencer. Beard argued, "It is generally recognised that society is more than a mere aggregate of individuals; that the individual is not only a sharer in the life of the organism, but is also capable of modifying by his inter-social activities its structure, function and lines of development."[25] Rejecting Spencerian individualism, Beard called instead for a rational, planned economy. Beard and other observers of human nature could use teleology to explain stability in the social organism, but this option was less acceptable to biologists. Thus the question remained: If the biological community were to be compared to an organism, could the struggle for existence explain the apparent stability of this organic entity? If so, exactly how did this occur? If not, what other mechanisms might be involved in maintaining stability?

The Lake as a Social Microcosm

The themes developed in Spencer's "Social Organism" were elaborated in ecological form in a classic essay written by Stephen A. Forbes. First published in 1887, "The Lake as a Microcosm" is generally recognized as one of the first statements of the ecological concept of the biological community.[26] So popular was this essay that it was reprinted in 1925, and it continued to be read and commented upon by ecologists for several decades thereafter. Writing during a period of professionalization and increasing specialization, Forbes was a transitional figure in the history of modern biology. Largely self-educated, he was one of the last great naturalists whose interests spanned the gamut of topics in traditional natural history: botany, entomology, ichthyology, and ornithology. At the same time, his seminal writings helped to define the newly emerging specialties of ecology and limnology.[27]

Born in Illinois to a poor farming family, Forbes's early education—one year at Beloit Academy in Wisconsin—was interrupted by military service during the Civil War. After serving in the Illinois cavalry, Forbes entered Rush Medical College, but he left without a degree after becoming "infatuated" with botany.[28] His early scientific research, particularly in entomology, was sufficiently impressive that he was named curator of the natural history museum in 1872 and professor of zoology at the Illinois State Normal University in 1875. But only after being appointed chairman of the zoology department at the University of Illinois in 1884 did Forbes receive a somewhat unusual academic degree. "It was also in 1884," Forbes later wrote, "that Indiana University gave me the degree of doctor of philosophy 'on examination and thesis,' entirely the product of private study, as I had taken no academic college course and had no bachelor's degree."[29] Shortly thereafter, at the height of his career, Forbes wrote "The Lake as a Microcosm."

In his famous essay Forbes drew a vivid picture of the aquatic environment and the interacting organisms living there, a picture strikingly reminiscent of Charles Darwin's entangled bank. According to Forbes, the natural order and lack of chaos that characterized this "little community" could be explained by two general ideas.[30] First, there was a *community of interest* even among predator and prey; each prudently acted to maintain the optimal population size of the other. "The interests of both parties," Forbes wrote, "will therefore be best served by an adjustment of their respective rates of multiplication such that the species devoured shall furnish an excess of numbers to supply the wants of the devourer, and that the latter shall confine its appropriations to the excess thus furnished."[31] Second, this well-ordered community had evolved and was maintained by the "beneficent power of natural selection," which, though destructive, promoted the common interests of the constituent species.

Reading Forbes's description of the aquatic community one is struck by the richness of description and the highly literary style of the essay. But one cannot help feeling that Forbes was struggling to develop an appropriate technical language with which to describe the interactions between aquatic plants and animals. In describing these interactions, Forbes relied upon a variety of metaphors: mechanical, organic, political, and economic. Perhaps the dominant image suggested by Forbes's essay is that of nature as a battlefield of each against all. Life in the lake was a "fearful slaughter" of prey by predators, a constant "scramble for food" among competing individuals, and a continual challenge of adapting to an endlessly fluctuating physical environment.[32] Within such an unstable environment few lived to maturity, but Forbes, like Darwin and Spencer, believed that this ceaseless strife was also a mechanism for insuring social harmony and progress:

> In this lake, where competitions are fierce and continuous beyond any parallel in the worst periods of human history, . . . where mercy and charity and sympathy and magnanimity and all the virtues are utterly unknown; where robbery and murder and the deadly tyranny of strength over weakness are the unvarying rule; where what we call wrong-doing is always triumphant, and what we call goodness would be immediately fatal to its possessor,—even here, out of these hard conditions, an order has been evolved which is the best conceivable without a total change in the conditions themselves; an equilibrium has been reached and is steadily maintained that actually accomplishes for all the parties involved the greatest good which the circumstances will at all permit.[33]

This natural equilibrium, however tenuous and imperfect, suggested other images to Forbes, both mechanical and organic. For Forbes, the lake was both a complex machine and an organism.[34] Species within the community were parts of a larger whole, and any change in one had ramifications for other parts and the entire community. From a careful analysis of the stomach contents of black bass, Forbes knew that this important predator relied upon numerous species of insects and crustaceans for food.[35] Directly or indirectly, it depended upon nearly every animal in the lake. This mutual dependence was a general rule in the microcosm, and the intricate interactions among species maintained a regularity and stability in the community as a whole. Life for the individual was a chaotic existence of ceaseless competition and predation, but at the level of the species this led to optimal population size, and at the level of the community it led to a stable equilibrium between predators and prey.

The term *community* that Forbes used to describe the interacting plants and animals in the lake became a fundamental ecological concept during the twentieth century by suggesting a close analogy between human affairs and biological processes. Forbes's lake was not only a microcosm of nature but also a reflection of American society. The economy of nature was dictated by the same law of supply and demand that served as an invisible hand in regulating the marketplace. In both instances, success went to the best adapted and most efficient competitor. "Just as certainly as the thrifty business man who lives within his income will finally dispossess his shiftless competitor who can never pay his debts," Forbes wrote, "the well-adjusted aquatic animal will in time crowd out its poorly-adjusted competitors for food and for the various goods of life."[36] However, Forbes's essay did not evince quite the same optimism in unregulated capitalism as Spencer's early writings. By 1883 Forbes's America had suffered through a recent economic depression, a decade of labor strife, and the uncertainties of a new industrial capitalism increasingly dominated by large corporations. Forbes's aquatic microcosm may have exhibited a harmonious balance, but this balance could be easily disturbed. For example, unpredictable changes in water level might lead to catastrophic death among vulnerable species in the lake.

Forbes's essay, so anthropomorphic in its description of life in a lake, was not aberrant; it was quite typical of proto-ecological literature. For example, a similar style was employed by the botanist Conway MacMillan in his early descriptions of plant communities. MacMillan had studied with Charles Bessey, an eclectic botanist and gifted teacher, who established one of the most influential American schools of ecology at the University of Nebraska.[37] After completing a master's degree at the University of Nebraska, followed by a year of additional study at Harvard and Johns Hopkins, MacMillan was hired as an assistant professor of botany at the University of Minnesota in 1887.[38] Four years later he became chairman of the department and state botanist, posts that he held until he resigned in 1906.

One of MacMillan's duties as state botanist was to complete a botanical survey of Minnesota, part of which appeared as an eight hundred–page list of species, *The Metaspermae of the Minnesota Valley* (1892).[39] Tucked in the middle of this ponderous description of regional flora was a brief discussion of the dynamics of vegetation, a discussion that anticipated important areas of research in early twentieth-century plant ecology. According to MacMillan, the apparent stability and permanence of the plant cover was an illusion; vegetation was actually in a constant state of flux. For economic botanists this fact became obvious when introduced weeds spread quickly at the expense of valuable crops. This was but one example of a general biological and social law: "Every individual plant must make its way in the world. It must either win new territory, maintain what it has already won, or cede its place of abode and growth to some plant better fitted to cope with the conditions peculiar to that particular spot. It thus happens that the flora of any region—that is to say the plant society of the region—is in the same condition of mutual interdependence and mutual competition that we discover in human society."[40] Competition, for MacMillan, was more than simply the war of each against all. It involved a complex set of interactions at a number of levels: the individual, the species, and the plant community as a whole. Individual plants, like humans, competed with one another, but they also cooperated by banding together in mutual self-interest against other groups of plants.

> Each species competes with those around it and in this competion [*sic*] the individuals might be said to stand shoulder to shoulder against the common foe, as may be seen in the united efforts of a human tribe or nation against some warring body. And again groups of species, having perhaps a common line of movement or a common need to be supplied, band themselves together and find arrayed against them other united groups of species competing for the same necessity or striving to move in the opposite direction.[41]

This form of high-level competition was most evident at the boundary between the forest and prairie, where the two great communities—each made up of hundreds of species—engaged in "silent warfare" over contested territory. Thus, like Darwin and Forbes, MacMillan interpreted the struggle for existence broadly. This process occurred at a number of levels and worked hand in hand with cooperation.

Themes and Metaphors

By about 1900 the major themes of ecological discourse were established: change and uniformity, instability and equilibrium, competition and cooperation, integration and individuality.[42] These did not constitute mutually exclusive positions but rather alternative preferences or guiding ideals. If the dominant themes of Darwin's work were competition and change, then this did not necessarily preclude a high degree of uniformity, stability, and interdependence in the natural world. Similarly, the stability of Forbes's aquatic microcosm did not reflect a static equilibrium. For the individual fish, the lake was a hurly-burly of endless strife, and entire populations might be imperiled by unpredictable fluctuations in the environment. Stability was an important concept for Forbes, but he was not a prisoner to some rigid, dogmatic commitment to equilibrium. Like the other proto-ecologists of the late nineteenth century he used this idea flexibly. This is an important point to emphasize. In his book, *Discordant Harmonies,* Daniel Botkin accuses Forbes and other early ecologists of viewing biological rhythms in terms of pendulum-like regularity. Forbes actually used this metaphor in his work, but he was careful to note that the amplitude of the biological pendulum in his aquatic microcosm was constantly altered by disturbing forces.[43] Stability and instability, like other thematic polarities, established a range of possible explanations; they did not define incommensurable positions or dogmatic schools of thought.

The most striking stylistic feature of the literature considered in this chapter is the rich use of metaphorical language. Scientists often dismiss metaphors as mere figures of speech, but it seems likely that these linguistic devices play important, constructive roles in scientific discourse.[44] Metaphors are explanations; when Stephen Forbes described the lake as a battlefield he was providing an explanation of something poorly understood (limnology) in terms of something well-understood by many members of his post–Civil War audience. Metaphorical descriptions suggest analogies, some perhaps strong enough to count as testable predictions. To claim that an aquatic community is an organism suggests a certain level of interdependence among its parts. Forbes, in fact, claimed that *every* member of the community was dependent upon every other.[45] Such extreme interdependence might exist in nature, but it also might not. This claim, a clear reflection of Forbes's organicism, was open to empirical refutation. Metaphors also suggest new questions or lines of research, some of which the originator may not fully recognize. To compare a biological community to a machine in the 1880s would have suggested somewhat different attributes to an audience than the same comparison made a century later during the age of computers. Finally, because they are so suggestive, metaphors may become easy targets for criticism. Opponents can emphasize incongruities and thus potentially discredit not only the metaphor but also the theory it represents. But as explanatory tools, hypothesis generators, heuristic devices, and targets for criticism, metaphors may stimulate the intellectual development of a new area of research.

Ecologists had a number of metaphors to aid in explaining the complex interactions and interdependencies that they encountered in nature: community, organism, and machine. All these were already used in the proto-ecological literature of the late nineteenth century. Despite its obvious limitations—it was inherently anthropomorphic, and it externalized the physical environment—the community became an important concept in ecology. The idea that plants and animals form a kind of community is natural enough. But "community" itself is a changing concept. During the period in which Forbes and MacMillan were writing, America was being transformed from a nation of relatively autonomous, rural "island communities" to an urbanized, industrial culture.[46] The informal social patterns of rural life were giving way to more centralized patterns of authority. Laissez faire, a doctrine that held such appeal for earlier generations, was being replaced with more hierarchical, regulative views of government and economy. The clash of social and economic ideas is reflected in the essays of Forbes and MacMillan. Indeed, the literary style of these writings highlights the influence of social thought upon science. Such influences would be partially, but never completely, obscured by the more technical style of twentieth-century scientific literature.

Today, the idea that plants and animals together form a kind of superorganism is anathema to most ecologists, but it was a popular mode of explanation for early ecologists. The concept of the organism implied organization, stability, and orderly change. As late nineteenth-century writers showed, however, organismal metaphors could also be used to discuss struggle, instability, and random disturbances. The belief that there is a kind of molecular struggle for existence within the body was commonly expressed. In Forbes's aquatic microcosm, which he compared to an organism, the stability of the whole only partially masked the uncertainties of struggle, conflict, and unpredictable change.

That organismal metaphors held such appeal for ecologists should not be too surprising. Organisms are natural objects familiar to all biologists. Through observation, classification, dissection, and experiment on this class of objects the neophyte biologist learns about organic structure and function. Organisms most clearly exhibit those characteristics seemingly unique to life: growth, development, metabolism, and reproduction. For ecologists during the early twentieth century organismal metaphors may have been particularly compelling for two other reasons.[47] Physiology, the queen of the life sciences during the late nineteenth century, had established an enviable repertoire of exact experimental techniques for studying organisms. Early ecologists often looked to physiology as a model of rigorous, experimental science. The cell theory, well-established by the late nineteenth century, provided a conceptual framework for discussing organic relationships, both in terms of part/whole and structure/function. Was it not reasonable to suppose that similar relationships existed between the individual organism and the biological community?

Mechanical metaphors played a similar, if somewhat less important, role in early ecology. In fact, the ideas of nature as a superorganism and nature as a machine were often used interchangeably.[48] The apparent equilibrium of a biological community could be compared to either the self-regulation in an organism or a machine controlled by a governor. In his essay on the aquatic microcosms, Forbes implied this relationship between self-governing machines, organisms, and biological communities. However, he did not fully develop his mechanistic descriptions of the lake. For much of the early history of ecology, mechanical metaphors remained an intellectual undercurrent. Only with the development of complex cybernetic systems during World War II did metaphors in ecology shift from organic to mechanical.[49]

Community, organism, machine: all these metaphors are consistent with Darwin's idea that nature forms a web of complex relations. But one might interpret Darwin in another way: perhaps his entangled bank is only an illusion. Perhaps the apparent order of nature is owing to populations independently adapting to a common physical environment. A community, if you care to use such a term, may be little more than a collection of autonomous populations that just happen to occupy the same place at the same time.[50] This "individualistic" view of nature, absent from the proto-ecological literature of the late nineteenth century, remained a minor eddy in the mainstream of early ecological thought. It too had to await the Second World War before it gained large numbers of adherents.

2

A Rational Field Physiology

There can be little question in regard to the essential identity of physiology and ecology.

—FREDERIC EDWARD CLEMENTS, *Research Methods in Ecology*

THE IDEA OF A GROUP of interdependent organisms, what Stephen Forbes referred to as a "community," became a central concept in ecology. Although Forbes and others discussed it during the late nineteenth century, the biological concept of community was most fully developed by midwestern botanists beginning about 1900. These botanists, among the first scientists to self-consciously identify themselves as ecologists, often claimed to be revolting against the genteel tradition of collecting and identifying specimens. Traditional botany, the young Frederic Clements claimed, "lends itself with insidious ease to chance journeys or to vacation trips, the fruits of which are found in vague descriptive articles."[1] In contrast, ecology was to be a rigorous, experimental science dealing with biological processes and their causes. Indeed, for Clements ecology was "nothing but a rational field physiology."[2] Midwestern plant ecologists were never quite so revolutionary as they sometimes claimed, and others were not always impressed with their vision of a new experimental science.

Critics sometimes dismissed plant ecology as a glorified agricultural science, but Clements and his contemporaries were interested in more than applied botany.[3] Ecologists, at the turn of the century, also were passionately interested in the broader biological problems of adaptation, development, and distribution. For these ecologists change was the primary characteristic of the natural world, and they called for a dynamic, process-oriented science that could explain this change. The physiological perspective that these biologists embraced had a pervasive influence upon the later development of ecological thought. Not only did this perspective suggest innovative methods for studying nature, but it also provided an explanatory framework that was both organic and mechanistic.

At the turn of the century, the midwestern United States provided a fertile environment—both physically and intellectually—for ecological studies. Most ecologists believed that fundamental biological problems could be studied best in natural laboratories: forests, lakes, dunes, and prairies. The frontier may have been coming to a close in 1900, but ecologists could still find pristine environments to study, and these natural laboratories were readily accessible from midwestern universities. Intellectually, the Midwest also provided a stimulating environment for the young science of ecology. New institutions such as the University of Chicago were breaking with traditional approaches to education.[4] As universities in the Midwest proliferated, biologists with new ideas about the nature of their science had unique opportunities to shape departments and research programs along nontraditional lines.[5] In a more subtle way, the midwestern environment may have influenced the way that ecologists approached their work. Writing at the turn of the century, the historian Frederick Jackson Turner suggested that the frontier was a powerful force capable of shaping human character.[6] Using a variation of this frontier thesis, Paul Sears later argued that ecological theory was significantly influenced by the midwestern environments within which early ecologists worked.[7] One need not accept this environmental determinism too literally to imagine the powerful impress that dunes and prairies made on the minds of early ecologists. It is perhaps not too surprising that the themes informing the historical writings of Turner at the University of Wisconsin—organic development, adaptation, evolution, and the interaction of organisms with their physical environments—also appeared prominently in the early literature of plant ecology.[8]

Henry Chandler Cowles and the Life History of Sand Dunes

Typical of this new breed of midwestern botanist was Henry Chandler Cowles. After graduating from Oberlin College in 1893, Cowles began graduate studies at the newly opened University of Chicago, an institution where he remained throughout his professional career.[9] During its early years, the University of Chicago was an exciting intellectual environment for an aspiring young scientist. President William Rainey Harper was luring many outstanding scientists to develop new research and teaching programs at the university.[10] Cowles initially began studying geology under T. C. Chamberlain, a noted geologist recently recruited from the University of Wisconsin. However, captivated by professor John Merle Coulter's discussions of plant life on the sand dunes of Lake Michigan, Cowles soon switched to botany. His dissertation described the long-term process of vegetational change, or succession, as it occurred on the dunes.[11]

Cowles's research was a stimulating mix of careful observation and rather speculative theorizing. He described in great detail the environmental conditions and the various "plant societies" that existed in the dunes: perennial herbs, shrubs, heath, coniferous forest, and deciduous forest. He then arranged these societies into developmental series. As Cowles envisioned the process, small embryonic dunes formed on the beach as sand washed up on shore. Some of these dunes were stabilized by colonizing plants, whose fibrous roots trapped the sand and prevented it from blowing away. The dune and its community of plants formed a symbiotic relationship, and over several hundred years both developed in a fairly predictable manner. Given proper environmental conditions the terminus of this developmental process, the climax community, was a large sandy hill covered with a deciduous forest dominated by beech and maple trees.

Cowles's research was inspired by earlier investigations of oceanic dunes in northern Europe, particularly those conducted by the Danish botanist Eugenius Warming.[12] Cowles shared Warming's enthusiasm for a physiological approach to the study of plant communities. Both men were committed to explaining the structure and distribution of plant communities in terms of the relationship between physical factors in the environment and physiological adaptations in plants. However, in a number of ways, Cowles's study differed from its European model. Despite his new-found love for botany and his interest in physiological adaptation, geology continued to hold a powerful attraction for Cowles. It provided a model for creating the new, dynamic ecology typified by his study of succession: "Such a study is to structural botany what dynamical geology is to structural geology. Just as modern geologists interpret the structure of the rocks by seeking to find how and under what conditions similar rocks are formed today, so ecologists seek to study those plant structures which are changing at the present time, and thus to throw light on the origin of plant structures themselves."[13] Geology also provided an important part of Cowles's explanation of succession. Changes in the topography of a region were the ultimate forces causing vegetational changes. Cowles's perspective was more than geological, however; he also employed the organic metaphors so common in American intellectual life at the turn of the century.

Cowles never claimed that a plant community was an organism, but organic analogies were common in his writing. Throughout his classic paper Cowles portrayed ecological succession as a developmental process. The dune began as an embryo, passed through a series of developmental stages, attained maturity, and eventually died. The fact that this complicated process did not always occur in exactly the same way did not alter the fact that the ecologist, studying a number of dunes, could describe the idealized life history of a dune.

Idealization is an important step in theory construction, and Cowles moved from observation to abstraction in a sophisticated manner. No single dune necessarily went through a particular series of developmental stages; the physical forces controlling succession were too unpredictable for that. "The simple life-history just outlined is the exception," Cowles wrote, "not the rule. . . . These processes of deposition and removal, dune formation and dune destruction, are constantly going on with seeming lawlessness."[14] Nonetheless, the simplified developmental scheme provided an explanatory framework for understanding the relationships among the various individual dunes making up a "dune complex." Using the metaphor of ontogeny Cowles systematized the seemingly chaotic changes in the soil and vegetation of the Indiana sand dunes.

Cowles's sand dune, like Darwin's entangled bank and Forbes's aquatic microcosm, was a scene of seemingly chaotic, lawless change, and at the same time, the site of orderly, law-governed processes comparable to those in a developing organism.[15] Both the predictability and the unpredictability of succession could be explained by the causal web underlying this developmental process. What Cowles described as a symbiotic relationship between the dune and its community of plants was not a simple interaction, but rather a shifting balance between two powerful agents of change. Plants could capture, stabilize, and modify the dune, but this outcome was not inevitable. Even though the dune provided the necessary resources for the development of vegetation, it also constituted a harsh and unpredictable environment for plants. Intense sunlight reflecting off the sand, lack of moisture, and a nutrient-poor soil, all provided extreme challenges to life on the beach. Most important, however, was the destructive sand-blasting effect of winds blowing off the lake. Living tissue could

hardly withstand such abrasion. The windward branches of trees were often stripped bare of soft tissue, leaving only a network of tougher fibers. Even more dramatic was the destructive effect on nonwoody plants. "Fleshy fungi have been found growing on the windward side of logs and stumps completely petrified, as it were, by sand-blast action"; Cowles noted, "Sand grains are imbedded in the soft plant body and as it grows the imbedding is continued, so that finally the structure appears like a mass of sand cemented firmly together by the fungus."[16] Wind not only destroyed individual plants, but it could also destroy whole plant communities. Under the influence of wind the sand dune was never a completely stabilized environment. Rather, this restless maze could break away, uprooting an established plant community and burying other communities as it advanced across the beach. This was not an uncommon event; the area was dotted with the "graveyards" of forests buried by wandering sand dunes. At any given time, therefore, the relationship between dune and plant community could develop into one of several possibilities. An uninhabited, wandering dune might be captured and colonized by plants. Together the dune and its inhabitants might grow and develop toward a climax community. Or the dune might break away from the stable relationship and destroy its symbiotic living partner in the process.

Competition played an important role in succession. The regularity of succession could be largely explained by replacing established species with better adapted competitors. For example, in certain moderately moist areas pines were replaced by oaks, not because the pines were poorly adapted to moist soil, but because oaks were better adapted.[17] Unlike Forbes's lake, however, competition on the sand dune was less a matter of struggle among individuals, than a struggle between the individual and its physical environment. The extreme conditions found on the dune posed a continual challenge to plant life, and only a few, well-adapted forms could meet this challenge. To successfully capture a wandering dune, a plant had to have an extensive system of roots to trap and hold sand. But even for those plants with networks of fibrous roots there was an ongoing struggle to hold sand against the eroding force of the wind. To be successful, therefore, the plant had to be capable of growth even when buried by the shifting sand. And, most important, it had to survive periodic exposure of its roots as the dune was eroded by wind. "In short," Cowles concluded, "a successful dune-former must be able at any moment to adapt its stem to a root environment or its root to a stem environment."[18] Thus, on the sand dune, adaptation often meant adaptability to a relentless and unpredictable physical environment. Cowles was particularly interested in the physiological adaptations that allowed individuals to successfully compete with this physical environment, but he was also interested in cooperation among individuals within a society of plants. A single plant was generally no match for a moving sand dune; the successful capture of the dune required the cooperative effort of many individuals.[19] Competition and cooperation, important causes of succession, both occurred on the dune.

Cowles's study of succession on the sand dunes of Lake Michigan became a classic in the literature of ecology. Its careful description and analysis became a model for Cowles's students and a source of inspiration for later ecologists, particularly those interested in ecosystems. Half a century later, Jerry Olson, another University of Chicago graduate student, returned to study succession on the dunes. His award-winning research placed dune succession within an explicit ecosystem context.[20] At about the same time, Eugene Odum, the dean of ecosystem ecologists, favorably compared Cowles's influence in ecology to that of Gregor Mendel in genetics.[21] Like many of his fellow ecosystem ecologists, Odum considered succession a fundamental ecological process.

Odum emphasized the dynamic nature of ecosystems, and his discussions of succession were rooted in the same physiological perspective that so attracted Cowles. Despite his enthusiasm for physiology, Cowles himself never fully developed this approach to research. His early work was primarily descriptive, and later in his career he published relatively little original research of any kind. As a young man, Cowles suggested that a plant community was analogous to an organism and that its internal processes could be studied physiologically, but he never made the transition to a truly physiological ecology. Ecology, for Cowles, remained firmly within the domain of natural history. Hiking across the dunes toward Lake Michigan, the ecologist could walk backwards in time, retracing the developmental history of the plant community.

Frederic Clements: The Physiological Perspective in Ecology

Intellectually, Cowles and Clements had much in common, and they both played important roles in establishing plant ecology in America. However, it is difficult to imagine two individuals so profoundly different in personality and scientific style. Cowles was a popular teacher whose warmth of personality and sense of humor were legendary.[22] He attracted a large and devoted group of students who continued the research program that he began during the 1890s. To a great extent, Cowles's legacy rests upon the intellectual lineage that he started at the University of Chicago. In contrast, Clements was often arrogant, priggish, and distant, inspiring little warmth even in those who knew him best. Although he trained a few students, most of his career was spent outside academia as a research associate at the Carnegie Institution of Washington. Unlike Cowles, who taught much but wrote little, Clements's influence arose from his voluminous writings; his books and articles touched on virtually every topic in ecology. Something of these differences is captured in photographs of the two great ecologists: Cowles, always looking a bit rumpled, often with a battered hat on his head and a boyish grin on his face, is a study in contrast with the stiff, neatly pressed, and unsmiling Clements (figures 1 and 2). Clothes may not make the man, but these contrasting portraits mirrored fundamentally different intellectual styles. Cowles often referred to the chaotic state of ecological thought as it existed early in the twentieth century, a situation he seemed to accept as inevitable. Ecology was to be a search for natural laws, but the nature that Cowles encountered on the sand dunes of Lake Michigan often appeared capricious.[23] In Cowles's ecology there remained a tension between order and disorder. Clements abhorred chaos in ecological thought as much as in his puritanical personal life. Out of his search for order emerged a theoretical ecology that was sweeping in its breadth and audacious in its simplicity.

When Clements entered the University of Nebraska in 1891, the botany department was gaining a national reputation. Charles Bessey was attracting bright young students and training them in the "new botany." Loosely patterned on a German educational model, Bessey's new botany emphasized experimentation and laboratory techniques, particularly the use of the microscope. However, according to Ronald Tobey, there was something uniquely American in Bessey's pragmatic approach to biological education.[24] Like other American intellectuals during the late nineteenth century, Bessey and his students were in revolt against what they perceived as the sterility of traditional education. Botany was to be learned not through rote memorization of textbooks but through experience in the laboratory and in the field. And it always had an eye toward the practical problems of agriculture and forestry.[25]

Bessey's new botany with its emphasis on experimentation and laboratory technique shaped Clements's approach to the study of ecology. Throughout his career, Clements liked to portray himself as a radical educator and a scientific innovator.[26] However, his vision of an experimental, physiologically oriented ecology did not crystallize immediately. Like Cowles's study of sand dunes, Clements's early research was descriptive. His doctoral research, done jointly with fellow student Roscoe Pound, was a fairly conventional study of regional vegetation. Inspired by the earlier geographical studies of Oscar Drude, Pound's and Clements's *The Phytogeography of Nebraska* catalogued species, described plant formations, and correlated these formations with general features in the environment.[27] But unlike the later Clements, he made no consistent attempt to measure environmental factors or to investigate causal relationships through experimentation. The book was a transitional work; the authors used ecology as one of several useful perspectives from which to study plant distribution. By 1905, Clements, then an associate professor at the University of Nebraska, reversed this relationship. In his first major ecological work, *Research Methods in Ecology*, a book that brought him international recognition, plant geography was presented as a small part of a more inclusive and rigorously experimental science of ecology. In the jargon of his new book, the descriptive geographical research that he had done as a graduate student was *reconnaissance*, a necessary but rather mundane prelude to more ambitious ecological experimentation.

The Plant Community as Organism

Running through Cowles's classic study of sand dunes is the idea that the plant community is like an organism; however, he never fully developed this suggestive analogy. Frederic Clements made this idea explicit and used it as a central concept in his theoretical ecology. For Clements the plant community really was a "complex organism," and succession was its life cycle. In turning to these organismal ideas, Clements avoided the naive anthropomorphism that Herbert Spencer succumbed to in the "Social Organism" and the traces of romantic imagery that lingered in the writings of Stephen Forbes, Conway MacMillan, and Cowles. Clements saw himself as a tough-minded professional struggling to create a technical vocabulary for ecology. The "complex organism" was not just a suggestive image; it was an important theoretical term for ecologists.

What did Clements mean when he claimed that the community is a kind of organism? It most certainly was not an organism in the same sense as a vertebrate animal or even a higher plant. What Clements seemed to have in mind as models for the community-organism were much simpler plants and animals, perhaps what we would refer to today as protists.[28] But even these models were not to be taken too literally. The similarities between simple organisms and complex organisms were not to be found in naive isomorphisms; parts of a forest were not precisely comparable to any anatomical structure. The simple organism and the community had in common a number of general biological characteristics. The community was an organic entity made up of interacting parts, much the way an individual was composed of interacting cells. It had spatiotemporal continuity, and it developed in a fairly predictable manner. Finally, the community had a kind of physiology, a set of processes through which it interacted with the physical environment to maintain a dynamic equilibrium. The community was capable of adapting just as any organism did.

Given the historical context within which he was working, Clements's suggestion that a plant community is a kind of organism was quite unremarkable. Organismal analogies had long been popular, and they continued to be characteristic of the intellectual landscape of early twentieth-century America.[29] Clements, however, was unusual in the way that he tied his organismal concept to a broader physiological perspective. Above all, Clementsian ecology was the study of *processes*, and physiology provided a successful model for ecological methods and explanations. Clements considered physiology to be the paradigmatic example of a rigorous, experimental science. If ecology was to become "a rational field physiology," then ecologists would need to develop equally rigorous methods for studying plants outside the laboratory. One purpose of *Research Methods in Ecology* was to acquaint ecologists with new quantitative and experimental techniques. Physiological theories, notably cell theory, provided an explanatory model for ecologists. Just as the physiologist could explain the functioning organism in terms of cellular activity, Clements hoped to explain the functioning of the "complex organism" in terms of the activities of its parts.

Late in his career, Clements dabbled in philosophical holism, but his physiological perspective actually reflected an extreme form of mechanistic reductionism. At all levels—individual, species, or community—Clements explained change in terms of simple, stimulus-response reactions. The physical environment acted and organisms reacted. By the time that Clements began writing, physiologists were moving away from such simplistic explanations, and the physiologists who read *Research Methods in Ecology* were universally hostile toward it.[30] Certainly today it is easy to smile at his naive mechanistic ideas.

Although he was wrong in the details, Clements provided future ecologists with a compelling intellectual approach to research. As we see in later chapters, other ecologists also looked to physiology, both for methodological and explanatory models. For now, however, we must examine Clements's physiological approach in greater detail.

Adaptation, Evolution, and Succession

The operation of Clements's organismal concepts and his broad physiological perspective can be seen in the way that he explained individual adaptation, speciation, and succession—three processes that he considered closely related. In *Research Methods in Ecology* he discussed several examples of adaptation to the physical environment. For example, he described what he believed to be the causal chain linking light intensity, photosynthesis, and the gross morphology of leaves.[31] An increase in light intensity (a "stimulus") caused a proportionate increase in the rate of photosynthesis (a "response"). Within the cell, this caused an increase in the number and size of starch grains. More important, the number of chloroplasts increased, optimizing the absorption of light.[32] These intracellular changes caused changes in the arrangement of cells and tissues and ultimately led to gross morphological changes in the leaf. In retrospect, it is easy to dismiss this as speculation, and Clements himself admitted that no conclusive experimental evidence supported his hypothesis. However, he did cite some indirect evidence to support his claims. It is a well-known fact that shaded leaves and sun-exposed leaves, even on the same plant, frequently exhibit distinct morphological features. As Clements attempted to demonstrate through microscopic examination, these gross changes were correlated with changes at the cellular and subcellular levels.

From this example it is clear that adaptation meant something more than the Darwinian fit between organism and environment. For Clements it also meant the physiological process of adjustment of which all organisms are more or less capable. This physiological adaptation had important evolutionary implications. As a neo-Lamarckian, Clements believed that environmental changes could directly cause the evolution of new species. He attempted to demonstrate the inheritance of acquired traits by transplanting low-altitude species into experimental gardens located on Pike's Peak in Colorado. As the transplants developed in their new habitat they took on characteristics typical of alpine plants, and in some cases Clements claimed that they became indistinguishable from species native to the mountain.[33] He concluded that by modifying the environment of a plant he could artificially induce speciation within several generations.

Clements's experimental neo-Lamarckism was within the mainstream of evolutionary biology during the first decade of the twentieth-century when he began his work, but much less so in 1945 when he died. His later career, discussed in chapter 3, increasingly became a quixotic attempt to document his evolutionary claims. The point I stress here, however, is not the long-term significance of Clements's evolutionary views, but rather the breadth of his physiological perspective. Beginning early in his career Clements proposed a unified mechanical scheme to explain both physiological and evolutionary adaptation. During the course of a single generation, individual plants adapted physiologically to changes in the environment. Over the course of several generations, species evolved in response to persistent changes in the environment. According to Clements, the same type of reasoning could explain the successional changes in plant communities.

Clements's reputation rests primarily upon his contribution to the study of succession. He outlined his theory of succession in *Research Methods in Ecology* (1905) and expanded these ideas in his most important book, *Plant Succession* (1916). This massive tome immediately became the definitive work on the subject, and today it remains a point of departure for many discussions of succession. For Clements, succession, a complex process of development, led from an embryonic community, through a series of stages, to the mature climax community. Despite its complexity, this developmental process could be reduced to a few simpler processes: plants invaded an area, they competed, they reacted to the physical environment, and they modified it.[34] Each process could be understood in terms of simple stimulus-response mechanisms.

Succession began when species invaded a previously uninhabited area. The success of the various migrants in establishing themselves depended upon their competitive abilities. But this was primarily indirect competition, more physical than biological. "Competition," Clements wrote, "is purely a physical process. With few exceptions . . . an actual struggle between competing plants never occurs. Competition arises from the reaction of one plant upon the physical factors about it and the effect of these modified factors upon its competitors."[35] Thus, for example, water absorbed by one plant was unavailable to others. Although such competition acted only indirectly on individuals, it played a decisive role in structuring the community: "The inevitable result is that the successful individual prospers more and more, while the less successful one loses ground in the same degree. As a consequence, the latter disappears entirely, or it is handicapped to such an extent that it fails to produce seeds, or these are reduced in number or vitality."[36]

The composition of a community at a given time reflected the relative adaptation of various species to a particular physical environment. However, this composition was not static; each stage in succession was characterized by a different set of species. Invasion and competition alone could not explain this dynamic nature of the community; another process was also involved. As plants reacted to their physical surroundings they modified important environmental factors. For example, by shading previously bare ground, pioneer species increased the moisture of the soil. This change in an important physical factor allowed new invaders to become established, which then altered the competitive balance in the community. Thus species were often replaced as an indirect result of the very environmental changes that they had caused. "The reactions of the pioneer stages may be unfavorable to the pioneers," Clements wrote, "or they may merely produce conditions favorable for new invaders which succeed gradually in the course of competition, or become dominant and produce a new reaction unfavorable to the pioneers."[37] In either case, the pioneer species were replaced by a new assemblage of plants. This developmental process continued until a climax community was established, a community that he described as "more or less permanent." Unless some external disturbance disrupted this process, the eventual establishment of the climax was as inevitable as the development of an adult plant from a seed.[38]

The persistence of the climax community could be explained in a number of ways. Through successive modification of physical factors such as light and moisture, the community progressively stabilized its environment. In contrast to early successional stages, which were in a constant state of flux, the climax was in equilibrium with its physical environment. As a result, the climax community formed a kind of biological barrier to further invasion; potential invaders could rarely compete successfully with established species. Once formed, this climax could persist indefinitely. According to Clements, "such a climax is permanent because of its entire harmony with a stable habitat. It will persist just as long as the climate remains unchanged, always providing that migration does not bring in a new dominant from another region."[39]

Equilibrium and the Climatic Climax

No aspect of Clementsian ecology has proven so controversial as his ideas on climax. A later generation of ecologists reacted against what they referred to as the Clementsian "monoclimax" concept, the idea that within a given climatic region succession always ends in a single type of community. Historians have also criticized Clements for his apparent determinism. For example, J. Ronald Engel argues that Clements accepted Herbert Spencer's deterministic worldview, a view that Engel compares unfavorably with Henry Chandler Cowles's belief in the flexibility and indeterminacy of succession.[40] Clements was a determinist of sorts, but the monoclimax is a parody of Clementsian thought. Of course, a parody requires something to imitate, and Clements's pedantic style lent itself to easy ridicule. But critics have ignored the important qualifications that Clements added to his theory. Clements was not some naive, armchair theoretician. Although deeply committed to his theories of succession and climax, he was a keen observer who knew about the complexities of nature.

Henry Chandler Cowles once characterized the developing equilibrium between plant community and physical environment as "a variable approaching a variable, rather than a variable approaching a constant."[41] Clements refused to go that far, but he, too, held a dynamic concept of equilibrium. The community was an organism, and like all organisms it was constantly adjusting to environmental fluctuations. "The most stable association is never in complete equilibrium. . . . Even where the final community seems most homogeneous and its factors uniform," Clements warned, "quantitative study by quadrat and instrument reveals a swing of population and a variation in the controlling factors. Invisible as these are to the ordinary observer, they are often very considerable."[42] External factors might drastically upset the equilibrium between the community and its environment. No community, even the climax, was completely closed. There was always the possibility that a foreign species might successfully invade the community.[43] Natural disasters or human interference could also modify climax patterns. Forest fires, logging, erosion—any one of these might damage or destroy the climax. In these damaged areas succession would begin again, but the overall result would be a landscape resembling a mosaic of climax and subclimax vegetation.

Clements's little-known study of forest fires in Estes Park is a case in point.[44] Periodic fires in the area often prevented the establishment of the theoretical climax forest, a forest dominated by Engelmann

Spruce. Lodgepole pine, an early successional species particularly well-adapted to seeding burned areas, sometimes persisted as the dominant species indefinitely. This was also true of aspen, which could quickly regenerate from underground roots after a fire. From experiences such as this, Clements knew that nature was complex; vegetation formed a mosaic, not a monotonous continuum. But ecology had to do more than simply describe this mosaic; it had to explain it. For Clements the concept of organic development provided the explanation.

The Individualistic Challenge

One could, of course, argue that Clements's particular explanation was badly misleading, that, even ignoring complicating factors, succession is not analogous to development and the community is not analogous to an organism. Precisely this charge was made by Henry Allan Gleason.[45] Like Clements, Gleason was born and raised in the Midwest. After completing bachelor's and master's degrees at the University of Illinois, he went on to receive the Ph.D. from Columbia University in 1906. He then taught at the University of Michigan for ten years, after which he moved to the New York Botanical Garden, where he remained for the rest of his career. Until the late 1960s he continued to publish papers on diverse topics in ecology, taxonomy, and plant geography.

In a series of short papers written over a twenty-year period, Gleason put forward what he referred to as the "individualistic concept" of the plant community.[46] Gleason claimed that the similarities between succession and ontogeny were superficial; succession was not a developmental process in any meaningful sense. Rather, this much less deterministic process depended to a large extent upon random events. As a consequence, the plants found in a particular area did not form an organic entity, but simply an assemblage of individuals.

Gleason based his reasoning on three premises. Environmental factors, particularly physical ones, always vary both in space and time. Each species of plant has a range of environmental tolerances, as does each individual member of the species. Plants tend to disperse seeds randomly. Thus, according to Gleason, the distribution of plants in any particular area was the result of fortuitous immigration and environmental selection. As the environment changed, so did the distribution of various species of plants. Gleason suggested, therefore, that succession was nothing more than a statistical replacement process. Better adapted species gradually replaced less well adapted ones, but replacement also occurred by the more random process of seed dispersal.

Given this indeterminism in plant distribution, what then was the status of the plant community? Certainly not objective units, Gleason argued, but "merely abstract extrapolations of the ecologist's mind".[47] If environmental factors varied continuously in space and time, if every species (indeed, every individual) had a unique range of environmental tolerances, and if immigration were fortuitous, then ecologists would often find plant communities with poorly defined boundaries. In general, species would be distributed independently across the landscape, and any two geographical areas, no matter how small, would contain slightly different assemblages of species. For Gleason, the biological community was little more than a coincidental assemblage of independent species sharing an area arbitrarily defined by the ecologist. "In conclusion," he wrote, "it may be said that every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements."[48]

Much has been made of the "Clements-Gleason controversy." Gleason liked to portray himself as an "ecological outlaw," and a later generation of ecologists popularized this image of Gleason as the embattled critic of ecological dogma, a critic whose ideas were later vindicated by rigorous experimental testing.[49] Such stories should not be given too much credence; within the historical context of pre–World War II ecology, the controversy amounted to very little. In his two most famous articles, Gleason never mentioned Clements's work directly. And Clements, who held Gleason in rather low regard, never responded to the younger ecologist's critiques.[50] But why was the individualistic concept so unpopular prior to World War II? To claim that ecologists of the 1920s and 1930s were dogmatically committed to Clementsian ecology is historically false. But even if true, it would not serve as an intellectually satisfying historical explanation. The questions still remain: Why were ecologists so committed to Clementsian organicism? And why did they find the individualistic concept unsatisfactory?

I suggest a number of alternative explanations. One explanation is institutional. Other ecologists supported the individualistic concept,[51] but prior to World War II none of these biologists developed an effective research program. Gleason may have thought that the individualistic concept was important, but he did not pursue it very far. He never collected data to support his claims, and his theoretical writings on the subject were limited to three short papers. As we shall see in chapter 3, Clements was a more astute "empire-builder" than his critics. During the 1920s he mustered the considerable resources of the Carnegie Institution of Washington to effectively promote his organismal ideas.

Politics was only part of the equation, however. There were also sound intellectual justifications for rejecting Gleason's individualistic concept. Lack of data was one. To an empiricist, Gleason's theoretical sketches would have compared rather unfavorably with the massive body of information collected in Clements's *Plant Succession.* Theoretically too, Gleason's argument was flawed. The suggestion that communities are not organisms *because* they lack distinct boundaries is an obvious non sequitur. Humans and some other animals may have rather definite external boundaries, but many other types of organisms do not; this distinction was pointed out by organismal thinkers both before and after Gleason's day.[52] In a broader sense, Gleason's concept lacked a convincing theoretical justification. For many biologists today, the individualistic concept is attractive because it fits nicely with recent theoretical trends in population ecology. Gleason was no population ecologist, however, and the apparent modernity of his ideas is deceiving. Evolution may have been implicit in his arguments, but Gleason did not use natural selection to justify his claim that ecology could be reduced to the activities of independent individuals. Nor did he refer to the theoretical population ecology or population genetics that was beginning to develop during the period in which he was writing. Clementsian ecology, whatever its problems, did have a well-developed theoretical foundation. In short, without substantial data or a satisfactory theoretical foundation, Gleason was asking his readers to abandon an apparently successful approach to research. Not surprisingly, even some ecologists who were highly critical of certain aspects of Clementsian ecology refused to embrace the individualistic concept.

One can get some sense of the response to Gleason's ideas from a student notebook of Raymond Lindeman.[53] Lindeman went on to write one of the formative papers in ecosystem ecology, but in 1937 he was a beginning graduate student in W. S. Cooper's plant ecology course at the University of Minnesota. Cooper's course was a mixture of lecture and discussion; the discussions often continued informally at the Cooper home. Cooper, a University of Chicago graduate, stressed the importance of carefully describing successional patterns and discovering the laws governing these patterns. The organismal concept was important, too, although Cooper believed that Clements pushed it too far. Gleason's paper was thought provoking but flawed. From the class discussion, Lindeman wrote down a long list of criticisms. Gleason's emphasis on accident and coincidence seemed to rule out the possibility of general laws of succession. The idea that a community is only a chance collection of individuals seemed unreasonable. Indeed, Gleason's heavy emphasis on randomness and indeterminacy seemed unjustifiable. Most important, the idea that indefinite boundaries vitiated the concept of community seemed untenable. "Do not transitions occur between everything?" Lindeman noted. "Then why throw out the idea of community because it can't be sharply defined?" Like most of his contemporaries Lindeman did not accept Clementsian ecology in its entirety, but he did believe that useful parallels existed between organisms and communities. From Cooper, he imbibed modified Clementsian ideas of succession, climax, and equilibrium, and he accepted the Clementsian notion that ecology is the study of physiological processes—ideas that later found expression when he attempted to define the scope of ecosystem ecology.

Succession and the Physiological Perspective in Ecology

The history of scientific controversies is not always neat and tidy, with clear winners and losers. The continued influence of Clementsian ideas, even after their apparent defeat, is a case in point. Shortly after World War II, Gleason's individualistic concept was partly vindicated by the field studies of a number of ecologists. Using a new technique, gradient analysis, John T. Curtis and his students at the University of Wisconsin and Robert H. Whittaker at the University of Illinois demonstrated that in many cases communities lacked clearly defined boundaries. As Gleason had predicted, populations scattered along environmental gradients formed continua rather than discrete units. Succession did not appear to follow neat linear sequences, and the climax seemed an indefinite mixture of species. "Climaxes are relative," Whittaker wrote, "and there are all degrees of climaxness."[54] For Whittaker and most later ecologists, the climax was a mosaic of vegetation, an entity definable only in statistical terms. During the 1950s Whittaker became an outspoken critic of Clementsian ecology. He and others often portrayed their work as destroying a Clementsian paradigm.[55] But Whittaker's work itself provides a good example of the tenacity of Clementsian ideas. When he discussed the structure of communities, Whittaker was an avowed Gleasonian individualist.

However, when he discussed the *processes* that occur in communities and ecosystems, Whittaker often slipped back into more organic or physiological descriptions: populations were parts of a larger whole, and each played a specific functional role to maintain the integrity of that whole.[56]

Much of Clementsian ecology has not stood the test of time. His continued belief in the inheritance of acquired traits, long after it was rejected by most other biologists, was aberrant. His mechanistic notions of cause and effect were considered simplistic even by many of his contemporaries. His insistence that succession is always progressive was also rejected by many ecologists of his day. His ideas of climax and the organic unity of the community were more influential, but they too have been modified or abandoned. Yet, despite all this, Clementsian thought has been enormously influential. As even his critics admitted, the very scope and systematic nature of Clements's work integrated ecological thought, and it stimulated both further research and criticism.[57] More important, Clements emphasized the importance of process in ecology, and he suggested a useful physiological perspective for studying it. This had a powerful influence on the development of ecology.

Few ecologists after World War II believed that a community or ecosystem really was an organism, but in important ways they continued to believe that these higher level systems behaved somewhat like organisms. Succession was the paradigmatic example. Although the Clementsian explanation was wrong in its details, the general idea that succession is a developmental process continued to serve as an important heuristic argument and a useful framework for explanation.[58] The physiological perspective suggested other important analogies between organisms and higher level systems. After World War II ecosystem "metabolism" and "homeostasis" became important areas of ecological research. Clements never considered these ideas, but they fit neatly into his general view that ecology was to be "a rational field physiology."

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An Ambiguous Legacy

One's success as a scientist can be measured more by the number of people he or she gets to work on new problems than by the correctness of specific research results.

—DAVID M. RAUP, *The Nemesis Affair*

The man who states a general theory which leads subsequent workers along the most fruitful lines of research performs a service which is fundamental to the progress of science.

—A. G. TANSLEY, "Frederic Edward Clements, 1874–1945"

FREDERIC CLEMENTS is an enigmatic historical figure. Universally recognized as one of the founding fathers of ecology, he has, nonetheless, become a convenient "fall guy" for some modern ecologists.[1] During his lifetime Clements's opponents ridiculed his ideas by characterizing them as "flights of fancy," "fairy tales," and "laughable absurdities."[2] Yet much to the consternation of modern critics, these same Clementsian ideas persist in modified form today.[3] How can one explain this ambiguous legacy? The story of the Clements-Gleason controversy, so popular among ecologists today, provides few insights. Indeed, the answer to this question is not found in intellectual comparisons removed from social context. The ambiguities surrounding Clements's historical reputation are better explained by considering the fate of the research group that he formed during the second decade of the twentieth century.

In its details, Clementsian ecology was badly flawed. But being wrong, perhaps even being egregiously wrong, is not antithetical to good science. Most scientists are wrong most of the time, and even great scientists turn out to be wrong much of the time. What is really