From: P.J. Bowler, I.R. Monry, Making Modern Science (UCP: 2005).

CHAPTER 9

ECOLOGY AND ENVIRONMENTALISM

AT FIRST SIGHT IT MIGHT SEEM OBVIOUS that the two topics listed in the title above should be linked together. The environmentalist movement has sought to warn of the dangers posed by humanity's evermore powerful efforts to exploit the world and its inhabitants through industry and intensive agriculture. It points to the increasingly common catastrophes that can be attributed to the uncontrolled exploitation of the world's resources and notes that we are now witnessing a mass extinction of geological proportions caused by the destruction of species' natural habitats. If we are not careful, the environmentalists warn, we shall wipe ourselves out by rendering the whole world uninhabitable. To make this point they sometimes call on the science of ecology, which seeks to describe and understand the relationships between organisms and their environment. Indeed the term "ecological" is often taken to mean "environmentally beneficial," as though the science went hand in hand with the social philosophy that seeks to defend the natural world (see the title of Bramwell's 1989 book, which is actually about environmentalism). Many assume that ecology is a science created by environmentalists to provide them with the information they need about the balance of nature and the ways in which disturbing influences such as human exploitation upset and ultimately destroy that balance. Such an interpretation of the origins of ecology would take it for granted that the science is based on a holistic worldview that seeks to understand how everything in nature interacts to produce a harmonious and self-sustaining whole. Ecology is the science behind James Lovelock's image of the earth as "Gaia"-a sustaining mother to all living things who will not hesitate to discipline one of her children if it gets out of line and threatens the whole.

One pioneering study by Donald Worster (1985) sought to present such a unified picture of the origins of both environmentalist thought and scientific ecology. But subsequent work has uncovered a more complex and far less coherent pattern of relationships. To a large extent, the environmentalist movement has opposed modern science as the handmaiden of industrialization, seeking its image of nature in a romantic impressionism rather than in scientific analysis. To the extent that it has had an impact on science, it has done so by encouraging a holistic methodology that openly challenges the materialistic and reductionist approach favored by the majority of scientists. There are thus some forms of scientific ecology that do draw inspiration from environmentalist concerns—but there are others that owe their origins to the reductionist viewpoint that is anathema to the romantic vision of natural harmony. Many of the first professional ecologists used physiology as a model, arguing that just as the physiologists saw the body as a machine, so they should apply a purely naturalistic methodology to studying how the body interacted with its environment. Some schools of ecology have remained resolutely materialistic, depicting natural relationships in terms more of a Darwinian struggle for existence than of harmony. Ecologists from these backgrounds are among the leading critics of Lovelock's efforts to depict nature as a purposeful whole that seeks to maintain the earth as an abode for life.

Modern historical studies force us to see ecology as a complex science with many historical roots. Indeed, it is not really a unified branch of science at all, since its various schools of thought have such different origins that they still find it hard to communicate with one another. Providing hard evidence for the environmentalist campaign is certainly not on most scientific ecologists' agenda. As in so many other areas, a historical study forces us to contextualize the rise of science, breaking down the more obvious links, such as those assumed to exist between ecology, holism, and environmentalism. Instead, we see the science emerging from a number of different research programs instituted in different places and times and for different purposes, some of them designed more to encourage the exploitation of the environment than to promote its protection. Far from originating as a unified response to a single philosophical message, ecology is a composite of many rival approaches that even today have not coalesced into a single discipline with a coherent methodology.

We begin with an overview of how science became associated with the drive to exploit the world's resources, then move on to an account of how the environmentalist movement emerged to counter this program. The second half of this chapter then outlines the emergence of scientific ecology from the late nineteenth century onward, showing how different research problems and different philosophical an ideological agendas promoted theoretical disagreement almost from the beginning.

SCIENCE AND THE EXPLOITATION OF RESOURCES

From the Scientific Revolution of the seventeenth century onward, the rise of science has been linked to the hope that better knowledge of the world would allow a more effective use of natural resources. The ideology promoted by Francis Bacon stressed the use of observation and experimentation to build up practical knowledge that could be applied through improvements to industry and agriculture. The world was depicted as a passive source of raw materials to be exploited by humanity for its own benefit. Even the methodology of science stressed the dominance of humanity and the passivity of the natural world: the experimenter sought to isolate particular phenomena so they could be manipulated at will. There was no expectation that everything might interact in a way that would negate the insights gained from the study of the particular. If the whole universe was just a machine, there was no reason why humanity should not tinker with individual parts for its own benefit. Carolyn Merchant (1980) sees this attitude as characteristic of an increasingly "masculine" attitude toward nature (see chap. 21, "Science and Gender"). By the end of the eighteenth century, this attitude was already bearing fruit as the Industrial Revolution got underway, and in the course of the following century the role that science could play in promoting technological development became obvious to all (see chap. 17, "Science and Technology").

At the same time, science was increasingly involved in the effort to locate and exploit natural resources around the world (fig. 9.1). The voyages of discovery undertaken by navigators such as Captain James Cook were intended to bring back information on the plants and animals of remote regions for Europeans to study and classify, but they were also intended to locate new territories that might be colonized. Sir Joseph Banks accompanied Cook on his first voyage to the South Seas (1768–71) as a naturalist. In his later capacity as president of the Royal Society, he helped to coordinate the British navy's efforts to explore and map the world, often with a view to discovering useful natural resources (MacKay 1985). The voyage of H.M.S. *Beagle*, which provided Darwin with crucial insights, was undertaken to map the coast of South America, a region vital to British trade. In the 1870s, the British navy provided a vessel, H.M.S. *Challenger*, for the first deep-sea oceanographic expedition (fig. 9.2). Although much information



FIGURE 9.1 A European naturalist in the tropics, from Pierre Sonnerat, *Voyage à la Nouvelle Guinée* of 1776. The naturalist describes the exotic creatures brought to him by the people of the region — an idealized relationship that was seldom maintained when European traders and colonists began to exploit the resources of these distant lands.



FIGURE 9.2 Deep-sea dredging equipment carried by H.M.S. *Challenger* on her pioneering oceanographic voyage from 1872 to 1876, from *Report of the Scientific Results of the Voyage of H.M.S. Challenger: Zoology* (London, 1880), 1:9. *Challenger* was equipped as a specialist survey vessel with on-board laboratories. The expedition scientists discovered a wealth of new marine species and disproved the widely held theory that the depths of the ocean were devoid of life. They also discovered manganese nodules on the deep-sea bed that are now seen as a potential source of minerals.

of scientific interest was generated, funding for marine science was increasingly provided in the expectation that there would be benefits for navigation, fisheries, and other practical concerns.

On land, too, there were many expeditions designed to explore remote regions to satisfy curiosity about the world (see below), but there were also explicit signs of science's growing involvement with imperialism. Many European nations established botanical gardens at home and in their colonies with the deliberate intention of identifying commercially useful plant species and studying how foreign species could be imported as new cash crops. Kew Gardens in London was the center of the British effort, under the direction of botanists such as Joseph Dalton Hooker, a leading supporter of Darwin (Brockway 1979). The cinchona plant, source of the antimalarial drug quinine and hence vital to European efforts to colonize the tropics, was transported via Kew from its home in South America to found commercial plantations in India. The rubber plant was smuggled out of Brazil despite a government prohibition to create the worldwide rubberproduction industry. North America was transformed as European farming methods were adapted to its wide range of different environments. By the early twentieth century, the Bureau of Biological Survey under C. Hart Merriam was coordinating deliberate attempts to eradicate native "pests" such as the prairie dog that destroyed the farmers' crops. Europeans and Americans were now interfering on an unprecedented scale with natural ecosystems, destroying native habitats and importing alien species as cash crops (for a survey of these developments, see Bowler [1992]).

THE RISE OF ENVIRONMENTALISM

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These developments were not without their critics, and gradually an articulate movement evolved to criticize the unrestricted exploitation — and often the consequent destruction — of the natural environment (McCormick 1989). The Romantic thinkers of the early nineteenth century celebrated the wilderness as a source of spiritual renewal and hated the industrialists who destroyed it for profit. Significantly, writers such as William Blake saw mechanistic science as a key component of the unrestrained exploitation of the natural world. A later generation of writers such as Henry Thoreau also celebrated the recuperative value of wilderness for a humanity increasingly alienated by an urban and industrialized lifestyle. In 1864, the American diplomat George Perkins Marsh wrote his Man and Nature to protest against the destruction of the natural environment. He warned that, contrary to early optimistic expectations, there was a degree of human destructiveness that nature might never be able to repair: "The earth is $fast^{1/\ell}\theta\delta^{2}\ell$ becoming an unfit home for its noblest inhabitant, and another era of equal human crime and human improvidence . . . would reduce it to such a condition of impoverished productiveness, of shattered surface, of climatic excess, as to threaten the depravation, barbarism and perhaps even extinction of the species" (Marsh 1965, 43). Marsh was not calling for a halt to all human interference but for better management that would allow the earth to retain its self-sustaining capacities. Partly as a result of his efforts, the U.S. government set up the Forestry Commission to manage the nation's resources, and eventually areas of woodland were set aside to be protected And aller from logging. Public concern also led to the designation of areas of outstanding natural beauty as national parks, Yosemite Valley in California in washed 1864 and Yellowstone in Wyoming in 1872. The Sierra Club, founded in 1892 by John Muir, was dedicated to the protection of wilderness areas. In Europe, where there was little true wilderness left to protect, efforts were nevertheless made to create nature reserves where stable environments that had existed for centuries could be conserved (on nature reserves in Britain, see Sheal [1976]).

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There was considerable tension between those who called for a more careful management of nature in order to allow resources to be renewed and an increasingly vocal movement that depicted all human interference as evil and potentially damaging to the earth as a whole. The former group was willing to call in science, in the form of the newly developed ecology, to help better understand the ways in which natural ecosystems would respond to human interference. But a more extreme form of environmentalism developed out of an alternative, more romantic vision of nature that, if it had any use for science at all, insisted that it must be a science based on holistic rather than mechanistic principles. This movement cut across all traditional political divisions and was by no means always sympathetic to a democratic approach to government. After all, the common people may well vote for more industrialization out of a short-sighted desire for more material goods. In Germany, a "religion of nature" often linked to the philosophy of the evolutionist Ernst Haeckel, became part of Nazi ideology and the Nazis created nature reserves on ground cleared of Jews and Poles sent to the death camps. Soviet Russia had a strong environmentalist policy until Stalin's drive for industrialization led to unrestricted exploitation of the country's resources (on European environmentalism, see Bramwell [1989]).

In America, there were debates between those who saw the "dust bowl" 10% on the Great Plains in the 1930s as part of a natural climatic cycle and those

who insisted that it was a consequence of the unsuitability of the prairies for farming. The latter position was increasingly typical of the more active environmentalist movement, which allied itself with those who saw the preservation of wilderness as essential for human psychological health, to say nothing of the health of the planet as a whole. In America, Aldo Leopold's Sand County Almanac, published posthumously in 1949, recorded the transition of a Wisconsin game manager into an environmentalist with an emotional and aesthetic attachment to wilderness. For Leopold, scientific ecology was not enough because it needed to be supplemented by an ethical commitment that recognized that all species have a right to exist, a right that should not be compromised by human expediency: "Conservation is getting nowhere because it is incompatible with our Abrahamic concept of land. We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect. There is no other way for land to survive the impact of mechanized man, nor for us to reap from it the esthetic harvest it is capable, under science, of contributing to culture" (Leopold 1966, x). Leopold's environmentalism did not rule out a role for the scientific study of nature, but that had to take place within a framework in which humanity was part of nature, not dominant over it.

Such an attitude has grown in influence, as more people have become aware of the dangers of the unrestricted exploitation of the environment. Rachel Carson's *Silent Spring* of 1962 highlighted the damage done to many species by the use of insecticides. Numerous environmental catastrophes have driven home the same message, although there are still significant differences between the ways in which different communities have responded. In America, despite the activities of those who cherish the wilderness, the public seems content to let corporate agriculture manipulate nature in the interests of producing cheaper food. In Europe, by contrast, the use of chemical fertilizers and insecticides has become unpopular, while genetic manipulation of food crops is restricted. In the Third World, however, genetic engineering is seen as perhaps the lesser of the two evils, since it might increase yields without leaving farmers dependent on expensive and potentially dangerous chemicals.

THE ORIGINS OF ECOLOGY

A distinct science of ecology only began to emerge at the end of the nineteenth century, although concepts we associate with the discipline had long been recognized. The Swedish naturalist Linnaeus wrote of the "balance of nature" in the mid-eighteenth century, noting that if one species increased its numbers due to favorable conditions, its predators would also increase and tend to restore the equilibrium. For Linnaeus, this was all part of God's plan of creation, and the natural theologians routinely described the adaptation of species to their physical and biological environment as an illustration of divine benevolence.

Systematic study of such relationships was also part of Alexander von Humboldt's project for a coordinated science of the natural world, which focused especially on the geographical factors that shaped different environments. Humboldt was impressed by the Romantic movement popular in the arts around 1800, with its emphasis on the ability of wilderness to inspire human emotions, but he insisted that a serious study of the natural world must use the scientific techniques of measurement and rational coordination. His aim was a science that focused on material interactions but interpreted them as parts of a coordinated whole in which each natural phenomenon was interlinked with all the others. He spent the years 1799-1804 exploring South and Central America, taking numerous scientific measurements in a variety of environments that were used to throw light on the interactions between their geological structure, physical conditions, and biological inhabitants. Humboldt made important contributions to geology — he was a follower of A. G. Werner and named the Jurassic system of rocks after the Jura Mountains of Switzerland (see chap. 5, "The Age of the Earth"). He also produced maps showing the variations of temperature and other climatic factors on a worldwide scale and others showing cross sections of mountainous regions illustrating how the characteristic vegetation changed with altitude (fig. 9.3). Humboldt's accounts of his South American voyage inspired many European scientists, including Darwin, and his emphasis on the earth as an integrated whole encouraged a whole generation to undertake systematic surveys of a variety of physical and biological phenomena. Under the influence of "Humboldtian science" biologists were taught to think in what we would now call ecological terms, looking for the ways in which the distribution of animals and plants was determined by the character of the soil and underlying rocks, the local climate, and the other native inhabitants of the region.

In the next generation, Darwinism, too, stressed the adaptation of the species to its environment but encouraged a more materialistic view of each population in competition not just with its predators but also with rivals seeking to exploit the same resources (see chap. 6, "The Darwinian Revolution"). Darwin also focused attention on biogeography, which illustrated how species adapted to new environments. It was the German Dar-



FIGURE 9.3 Alexander von Humboldt's schematic diagram showing the zones of vegetation at different levels on the South American mountain Chimborazo, from his *Essai sur la geographie des plantes* (1805). Humboldt's work helped to lay the foundations of ecology by showing how variations in the physical environment correlated with different forms of animals and plants.

winist Ernst Haeckel who coined the term "oecology" in 1866 from the Greek *oikos*, referring to the operations of the family household—the ecology of a region showed how the species there interacted to exploit its natural resources. But unlike Darwin, Haeckel adopted a nonmaterialistic view of nature in which living things were active agents within a unified and progressive world. The tension between the materialistic and holistic worldviews ensured that the science of ecology would be driven by theoretical disagreements from its inception. There were a number of different research programs, each trying to tackle the complex relationships be-

tween species and their environment in a different way. Because they began from different origins, they often adopted different theoretical outlooks.

The stimulus for the creation of the new biological discipline that would adopt the name ecology came from the breakdown of the descriptive or morphological approach to nature at the end of the nineteenth century. At that juncture, the emphasis was on experimentation, with physiology as the model, and a number of new biological disciplines arose in response to this challenge, including genetics. It was much harder to apply the experimental method to the study of how species relate to their environment, but there were several avenues that pointed the way to a more scientific approach to this topic. One was the increasing refinement of Humboldt's biogeographical techniques. In America, C. Hart Merriam of the Bureau of Biological Survey developed detailed maps showing the various "life zones" or habitats stretching from east to west across the continent. In 1896, Oscar Drude of the Dresden botanical garden published a fine-grained plant geography of Germany that showed how local factors such as rivers and hills shaped the vegetation of each region.

Plant physiology provided the model for other pioneers of plant ecology. Experimental studies had produced a much better understanding of how the internal functions of a plant operate, but by the end of the century a number of botanists began to realize that it would also be necessary to look at how the plant's physical environment affected these functions. This insight was especially obvious to those who worked in botanical gardens established in the tropics and other extreme environments, where the role of adaptation was crucial (Cittadino 1991). The founder of plant ecology, botanist Eugenius Warming, was trained in plant physiology in Denmark and had worked for a time in Brazil. He developed his approach as an alternative both to pure physiology and to the traditional focus of most botanists on classification (Coleman 1986). His Plantesamfund, published in 1895, was translated into German the following year and into English as *Oecology of Plants* in 1909. Warming could see how the physical conditions of an area determined which plants could live there, but he also realized that there was a network of interactions between the plants that were characteristic of a particular environment. These typical plants formed a natural community, each dependent in various ways on the others. The concept of a natural community had already been described by naturalists such as Stephen A. Forbes of Illinois, whose 1887 address to the Peoria Scientific Association, "The Lake as a Microcosm," had stressed that all the species inhabiting a lake were dependent on one another. It was a concept that was all too easily taken up by the opponents of materialism to argue that the

community formed a kind of superorganism with a life and purpose of its own. But Warming resolutely opposed this almost mystical view of the community; for him the relationships were just a natural consequence of evolution adapting species to the biological as well as the physical environment. He acknowledged that all the species were competing with each other in a constant struggle for existence and that when the original community was disturbed (as by human interference) there was no guarantee that the original collection of species would reestablish itself. If we cut down a forest, the trees may never get a chance to grow again because the soil has been modified in a way that prevents them from reseeding themselves. This view was also characteristic of one of the first American schools of ecology founded at the University of Chicago by Henry C. Cowles.

There was another American research tradition, however, that developed around a very different viewpoint. At the state university in Nebraska, Frederic E. Clements sought to put the study of grassland ecology on a more scientific footing (Tobey 1981). The European techniques were not suited to the vast uniform areas of the prairies, and Clements realized that in these conditions the only way to get really accurate information about the plant population was literally to count every single plant growing in a series of sample areas. He marked out measured squares or quadrats spread over a wide region and compounded the information to give a much more precise assessment of the overall population (fig. 9.4). By clearing quadrats of all vegetation, he was able to see how the natural plant community reestablished itself and became convinced that in these circumstances there was a definite sequence by which the natural or "climax" population was built up. Clements's Research Methods in Ecology (1905) publicized the new techniques, and the school of grassland ecology established itself, especially in institutions dealing with the practical problems of the farmers whose activities inevitably destroyed the natural climax grassland of the prairies. Clements was an influential writer and he promoted a philosophy of ecology that was very different from the materialistic approach of Warming and Cowles. He saw the natural climax population of a region in almost mystical terms: nature was predestined to move toward this community whenever it was disturbed, and the community had a reality of its own that required it to be seen as something more than a collection of competing species. Here was an ecology that seemed to derive from the romantic image of nature as a purposeful whole that resisted human interference, yet it was being used to give advice to the farmers whose activities had destroyed the natural environment of the plains.



FIGURE 9.4 Typical plant ecology survey, from John E. Weaver and Frederic E. Clements, Plant Ecology (New York: McGraw-Hill, 1929), 41. An area of overgrazed pasture at Lincoln, Nebraska, has been marked off in five-foot squares and the position of different types of vegetation noted: individual wolfberry shrubs are marked with an X, areas covered by bluegrass with vertical hatch, buffalo grass with cross hatch, and wheat grass left blank. The upper survey was taken in 1924, the lower in 1926, showing an expansion of the shrubs and a decrease in the area covered by bluegrass and buffalo grass. The small squares indicated in bold are quadrats marked off for a more detailed survey in which each individual plant would be counted.

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CONSOLIDATION AND CONFLICT

In the early decades of the twentieth century, the rival approaches to ecology pioneered by Warming and Clements gained enough attention for the area as a whole to become recognized as an important branch of science. But new developments continued the original tensions, and there was competition among the different research schools for control of its journals and societies and for access to government and university departments where it might flourish. In fact, despite a promising start, expansion was slow until after World War II. The British Ecological Society was the first ecological society to be founded, in 1913 (Sheal 1987), followed two years later by the Ecological Society of America (whose journal, Ecology, first appeared in 1920). But the new discipline's bid to establish itself in academic departments was slow, except in America, and even here the membership of the Ecological Society remained static through the interwar years. In Britain, pioneer ecologists such as Arthur G. Tansley had to struggle for academic recognition; Tansley spent some time as a Freudian psychologist and blamed the slow growth of ecology in part on the loss of promising young scientists in World War I.

In America, Clements's school of grassland ecology continued to flourish into the 1930s, when it provided support for the claim that the prairies should be returned to their natural climax of grassland to recover from the erosion of the Dust Bowl. The idealist notion of the climax community as a superorganism with a life of its own was linked by his student John Phillips to the holistic philosophy being popularized by the South African statesman Jan Christiaan Smuts, whose *Holism and Evolution* appeared in 1926. Smuts made an emotional appeal to a vision of nature as a creative process with inbuilt spiritual values and depicted evolution as a process designed to bring about complex entities whose properties were of a higher level than anything visible in their individual parts. In Britain, Tansley had to compete with South African ecologists wedded to Smuts's philosophy who were threatening to dominate ecology throughout the British Empire (Anker 2001).

Although Clements and his supporters tried to explain the Dust Bowl, the fact that the soil had disappeared effectively undermined their claim that the natural climax vegetation could reestablish itself. Other schools of ecology developed, especially in university departments that did not have to deal with the problems of the prairie farmers. Henry Allan Gleason and James C. Malin both challenged Clements's ideas by arguing that changes could take place in the vegetation of a region due to fluctuations in the cli-

mate and the natural invasion of species from other regions. In Britain, Tansley—who eventually gained a chair at Oxford—argued strenuously against Phillips's use of the superorganism concept, openly dismissing it as little more than mysticism. Yet Tansley used research methods very similar to those of the Clements's school, and it was he who coined the term "ecosystem" in 1935 to denote the system of interactions holding the species of a particular area together. For any European biologist, it seemed obvious that most apparently "natural" communities were to some extent the product of human activity, perhaps extended over centuries, so there was little point in trying to claim that a particular ecosystem had some sort of prior claim to be recognized as the only one appropriate for a certain area. Tansley and other critics also worried that promoting the idea of a superorganism would play into the hands of mystics who wanted to block any scientific study of the natural world. In continental Europe, an entirely different form of ecology based on the precise classification of all the plants in an area was developed, and in this the notion of a superorganism was simply irrelevant.

A clear indication of the fragmentary origins of ecology can be seen in the fact that it was not until the 1920s that systematic study of animal ecology began. But here, too, the tensions between the materialistic and holistic viewpoints immediately asserted themselves. At the University of Chicago, Victor E. Shelford applied Clements's approach to the study of animal communities and their dependence on the local vegetation. Also at Chicago, Warder Clyde Allee began to study animal communities on the assumption that cooperation between the members of the population is an integral part of how a species deals with its environment (fig. 9.5). Allee dismissed the Darwinian view of individual competition as the driving force of behavior and of evolution — he explicitly rejected the notion of a "pecking order" determining individuals' rank within the group. For him, evolution promoted cooperation, not competition, a view closely allied with the holistic philosophy characteristic of Clements's group. Allee and his followers also developed the political implications of their vision of natural relationships as an alternative to the "social Darwinism" that presented individual competition as natural and inevitable (Mitman 1992).

A very different approach was developed in Britain by Charles Elton, who worked at the Bureau of Animal Populations at Oxford from 1932 (Crowcroft 1991). His book *Animal Ecology* (1927) established itself as a textbook for the field and popularized the term "niche" to denote the particular way in which a species interacted with its environment. Elton had worked with the records of the Hudson's Bay Company that gave details of



FIGURE 9.5 Scheme of ecological relationships between species in the aspen parkland of Canada, from W. C. Allee et al., *Principles of Animal Ecology* (Philadelphia: W. B. Saunders, 1949), 513. Allee and his colleagues in the Chicago school of ecology stressed the harmonious interactions between individuals and species in order to minimize the role of the struggle for existence in both nature and human society. Their textbook was colloquially known as the "great AEPPS book" after the initials of its authors' names (Allee, A. E. Emerson, Orlando Park, Thomas Park, and K. P. Schmidt). fluctuations in the numbers of fur-bearing animals trapped over many years. These revealed occasional massive increases in numbers (plagues of lemmings are the classic example) caused when rapidly reproducing species outstrip their natural predators in a time of plentiful resources. The occurrence of such episodes made nonsense out of the old idea of a "balance of nature" and confirmed Darwin's Malthusian image of populations constantly tending to expand to the limit of the available resources.

Elton made common cause with Tansley and with the young Julian Huxley to promote their vision of ecology, which Huxley was also concerned to link with the new Darwinism emerging in evolution theory. By denying the existence of a natural ecosystem characteristic of any environment, their approach made it easier to see the natural world as something that could be adjusted to human activity through scientific planning. Such a vision had clear social implications and was popularized in the science fiction novels being written by H. G. Wells (who also collaborated with Huxley on a major popular work, The Science of Life, in 1931). At this point, however, they did not envisage ecology as a subject that could be analyzed using mathematical models, partly because the rapid fluctuations in population density observed by Elton seemed unpredictable. But others were becoming more interested in the possibility of using mathematics, perhaps by seeing an analogy between the behavior of individual molecules in a gas and of individual animals interacting with their environment. The American physical chemist Alfred J. Lotka published a book on this topic in 1925, and this approach was subsequently taken up by the Italian mathematical physicist Vico Volterra, who had become interested in predicting the fluctuations in commercial fish populations. In the late 1930s, the Russian biologist G. F. Gause performed experiments on protozoa to test the "Lotka-Volterra equations," and his efforts to substantiate the mathematical techniques would play a vital role in stimulating the expansion of ecology after World War II (Kingsland 1985). For the time being, however, there were many who shared Elton's suspicions, feeling that the unpredictable dynamics of natural population changes were an unsuitable field for the application of abstract mathematical models.

MODERN ECOLOGY

Ecology expanded rapidly in the 1950s and 1960s as the world became more aware of the pressing environmental problems created by human activity. But the pressure was not necessarily coming from environmentalist groups. Those who sought to control and exploit nature also wanted information that would help them manage the ever more complex problems that they were confronting (Bocking 1997). The ecologists exploited the new image of a more "scientific" approach made possible by the mathematical techniques developed by Lotka and Volterra before the war. They were also able to make common cause with the Darwinian synthesis now beginning to dominate evolutionary biology following the emergence of the genetical theory of natural selection (itself based on mathematical modeling of populations). A school of population ecology emerged based on the exploitation of the Darwinian idea that competition was the driving force of natural relationships. There was no overall theoretical consensus, however, because at the same time a rival school of systems ecology emerged, exploiting analogies between ecological relationships and the stable economic structures existing in human society. Here there was a renewed focus on the harmonious nature of communities, drawing not on the old vitalistic philosophy but on the models of purposeful natural systems created in cybernetics. When James Lovelock's Gaia theory extended this approach into something that looked like the old mysticism, he was violently criticized by most biologists for abandoning the materialist ethos of science and pandering to the romanticized image of nature favored by the extreme environmentalists.

The Lotka-Volterra equations reinforced the lessons of Darwinism by implying that in a world dominated by competition, the best-adapted species in any environment would drive all rivals to extinction. This became known as the "principle of competitive exclusion," which states that there can be only one species occupying a particular niche in a particular location. This principle was tested by David Lack, a student of Julian Huxley, in the case of "Darwin's finches" on the Galapagos Islands. Although Darwin had used these birds as a classic example of specialization, later studies had shown that there were often several different species feeding in apparently the same way on the same island. Lack showed that this was not the case because each species was actually exploiting a different way of feeding-just because they were all mingling together did not mean they were taking the same food in the same way. His book Darwin's Finches (1947) helped to establish the new Darwinian synthesis in evolutionism and the principle of competitive exclusion in ecology, while at the same time renewing interest in Darwin's role as the founder of the selection theory.

The British-trained ecologist G. Evelyn Hutchinson, who had moved to America in 1928, launched an attack on Elton's refusal to use mathematical models in animal ecology. He argued that where there were difficulties in applying the Lotka-Volterra equations, the best approach was to modify the mathematical models, not reject the technique altogether. Hutchinson wanted to use the mathematical models to unify ecology and evolution theory, as proclaimed in the title of his 1965 book The Ecological Theatre and the Evolutionary Play. His student Robert MacArthur went on to found a new science of community ecology based on Darwinian principles of struggle and competitive exclusion (Collins 1986; Palladino 1991). MacArthur used mathematical models to address questions such as how close the niches could be in a particular environment and whether the niches evolved along with the species. Like Lack, MacArthur became interested in the problems posed by the structure of populations on isolated islands. He teamed up with Edward O. Wilson to develop a theory that predicted that the diversity of species on an oceanic island was directly proportional to its area. The number of species was maintained by a balance between immigration and extinction, the latter always a threat to small isolated populations. Wilson became interested in the way in which different reproductive strategies would help or hinder a species trying to establish itself on a new island and subsequently went on to develop the science of sociobiology.

Hutchinson had other interests, however, and these helped to create a rival school of systems ecology based on very different theoretical principles. He wanted to study communities using not an organismic analogy but an economic one, which traced the flow of energy and resources through the system and sought to identify feedback loops that maintained the stability of the whole. This was an approach pioneered by the Russian earth scientist V. Vernadskii, who had coined the term "biosphere" earlier in the century. The concept of feedback loops was central to the new science of cybernetics founded by Norbert Weiner to explain the activity of self-regulating machines. Hutchinson imagined such feedback loops working on a global scale to maintain the various ecosystems in a stable state. He also saw an analogy between this model of nature and the economists' attempts to depict human society as a stable system based on the cooperative use of resources. Hutchinson's student Raymond Lindemann wrote an influential paper in 1942 analyzing the flow of energy derived from the sun through the ecosystem of Cedar Bog Lake in Minnesota. This model of energy flow was then built on by the brothers Howard and Eugene Odum, the founders of systems ecology. The Odums studied the energy and resource circulations in a wide variety of environments, basing their work on the assumption that large-scale ecosystems would have a substantial robustness in the face of external threats. Some of their studies were funded by the U.S. Atomic Energy Commission, anxious about the potential damage that might be caused by nuclear war or accident. Systems ecology saw the human economy as just one aspect of a global network of energy and resource consumption and presented models suggesting that all levels of the process could be managed successfully if the flow patterns could be understood. Howard Odum's *Environment, Power and Society* (1971) presented a technocrat's dream of a society carefully structured and managed so that it could maintain itself even in the face of the more restricted levels of resources that will be available to humanity in the future (Taylor 1988).

Community ecology and systems ecology thus represented rival visions of how to construct a model of the ecosystem, the one based on the Darwinian principle of competition, the other on a more holistic vision of apparently purposeful feedback loops. Philosophically and politically, they invoked very different implications about nature and human society. The result was a deep level of conflict in which each side dismissed the other as philosophically naive and scientifically incompetent. The later twentieth century thus did not witness a unification of ecology around a coherent paradigm. There were still different schools with different research programs, methodologies, and philosophies. The one thing they all seemed to agree on was that scientific ecology had to present itself as essentially materialistic, offering no opening for communication with the kind of nature mysticism favored by the extreme environmentalist movement. Although systems ecology retained a holistic approach reminiscent of Clements's vision of the ecosystem as an organism in its own right, the advent of cybernetics and the link to economics allowed even this school to distance itself from the old idealism.

It is in this context that we can judge the reaction to James Lovelock's Gaia hypothesis of 1979, in which the whole earth is seen as a selfregulating system designed to maintain life. Gaia is the name of the ancient Greek earth goddess and was chosen to imply that the earth is mother to all living things, humans included. Lovelock made no secret of his support for environmentalism, criticizing those who advocate unrestricted exploitation of nature by implying that Gaia will, if necessary, take steps to eliminate humanity if it becomes a threat to the whole biosphere. Lovelock had impeccable scientific credentials, having worked in the space program developing systems to monitor the earth's surface from satellites, but the rhetoric with which he presented his theory clearly touched a raw nerve with many scientists. Although apparently similar to the systems approach, Gaia seemed to go beyond the cybernetic analogy and return to the older organicism in which ecosystems (in this case the biosphere as a whole) have a real existence and can act on their own behalf to achieve their own purposes. Critics were not slow to point out these implications, dismissing

the whole theory as a perversion of science that pandered to the romanticism of the environmentalist movement. For Lovelock, it was as though a dogmatic scientific establishment had closed its ranks in defense of materialism: "I had a faint hope that Gaia might be denounced from the pulpit; instead I was asked to deliver a sermon on Gaia at the Cathedral of St. John the Divine in New York. By contrast Gaia was condemned by my peers and the journals, *Nature* and *Science*, would not publish papers on the subject. No satisfactory reasons for rejection were given; it was as if the establishment, like the theological establishment of Galileo's time, would no longer tolerate radical or eccentric notions" (Lovelock 1987, vii–viii). Nothing could more clearly indicate the gulf that still existed between scientific ecology (in all its forms) and radical environmentalism.

CONCLUSIONS

Although many people associate the term "ecology" with the environmentalist movement, we have seen that scientific ecology has a variety of origins, most of which were not linked to the defense of the natural environment. Science has more often been associated with efforts to exploit natural resources, and historical studies show that ecology emerged more from a desire to manage that process than to block it. At best, the majority of biologists have been concerned to ensure that humanity's engagement with the natural world does not do too much damage: sustainable yields are preferable to the wholesale destruction of a resource. Even those ecologists who imagined the ecosystem as a purposeful entity with a life of its own were willing to offer advice to farmers and others whose activities necessarily interfered with the untouched state of nature. In Europe, the whole idea of a purely natural landscape seemed meaningless, so ancient and so pervasive was the human role in shaping the environment. Although the more radical environmentalists can draw comfort from theories such as Lovelock's Gaia, they cannot lay claim to ecology as a science that inevitably lends support to their view that nature should be left untouched.

Equally interesting for the historian of science is the diversity of origins and theoretical perspectives from which the various branches of ecology emerged. Here was no single discipline shaped by a common research program and methodology. On the contrary, the movement toward what became known as ecology occurred in different places and at different times. The various locations of the scientists who became involved shaped the problems they sought to answer and hence the methodologies they thought appropriate. A technique that made sense on the open prairie of the American Midwest would have been inappropriate for the much-tilled landscape of Europe or the tundra of Hudson's Bay. Into these diverse environments came scientists with different backgrounds and interests; some were plant physiologists seeking to extend the experimental method to the interaction between plant and environment, some were biogeographers or taxonomists. All were driven by a determination to make the study of the interactions between organisms and their environment more scientific, but what they defined as "scientific" depended on their background and the problems they confronted. There was much suspicion to begin with over the application of mathematical techniques to modeling ecosystems. The majority of ecologists wanted to portray their science as materialistic, and this eventually led to a link with the revived Darwinism of the evolutionary synthesis. But there has been a persistent current of philosophical opposition to this movement, paralleling similar doubts in other areas of biology. Smuts's holism was by no means uncharacteristic of a nonmaterialist current of thought in early twentieth-century science. It certainly appealed to some of the early ecologists, and although that way of thought became less fashionable in the late twentieth century, its revival in the form of the Gaia hypothesis ignited a new level of debate. This debate reminds us of the gulf that still exists between the majority of scientists and the almost mystical vision of nature that has sustained the more radical environmentalist movement.

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