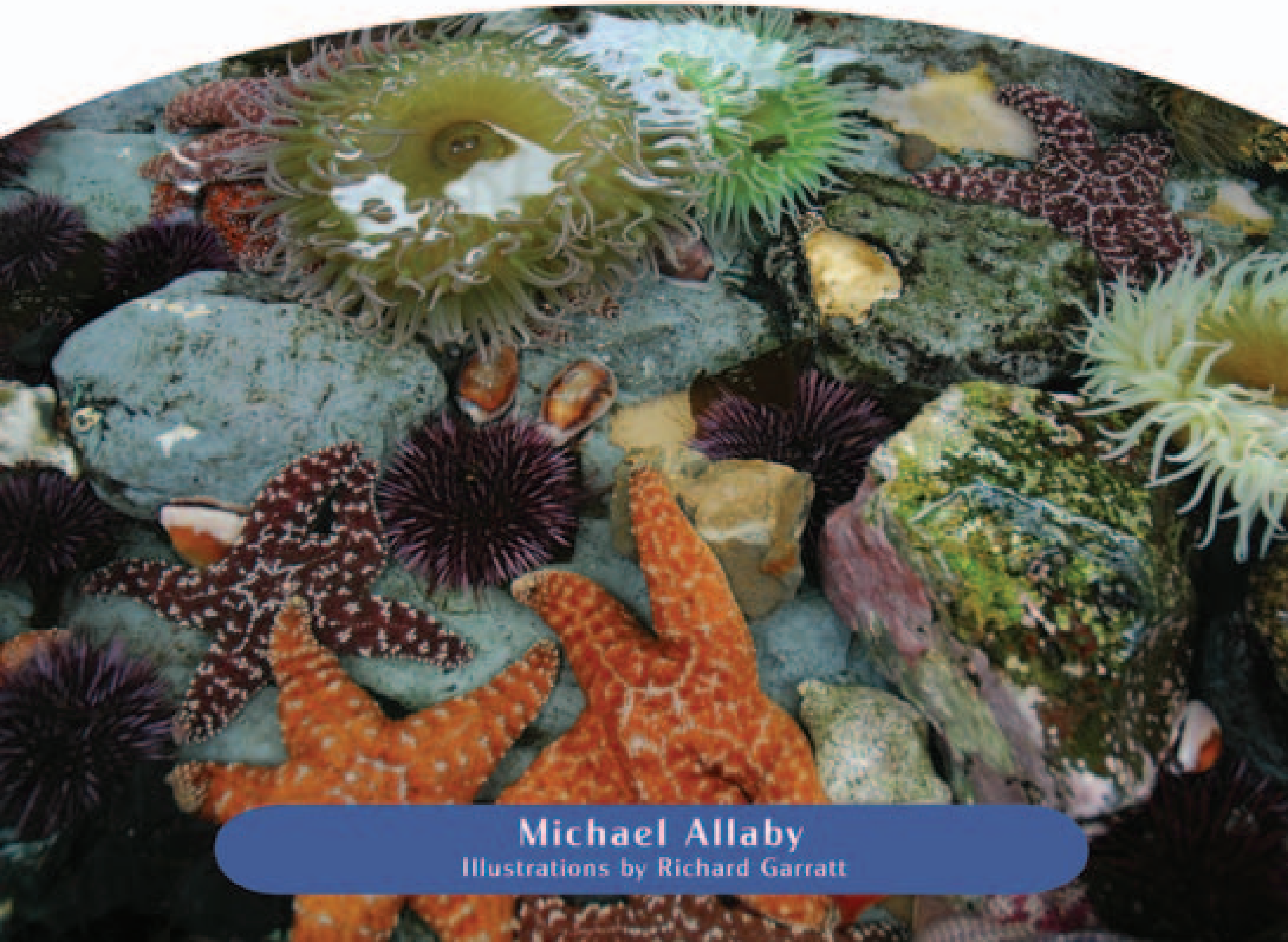
DISCOVERING the EARTH

# ECOLOGY

## Plants, Animals, and the Environment



**Michael Allaby**

Illustrations by Richard Garratt

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# PREFACE

Almost every day there are new stories about threats to the natural environment or actual damage to it, or about measures that have been taken to protect it. The news is not always bad. Areas of land are set aside for wildlife. New forests are planted. Steps are taken to reduce the pollution of air and water.

Behind all of these news stories are the scientists working to understand more about the natural world and through that understanding to protect it from avoidable harm. The scientists include botanists, zoologists, ecologists, geologists, volcanologists, seismologists, geomorphologists, meteorologists, climatologists, oceanographers, and many more. In their different ways all of them are environmental scientists.

The work of environmental scientists informs policy as well as providing news stories. There are bodies of local, national, and international legislation aimed at protecting the environment and agencies charged with developing and implementing that legislation. Environmental laws and regulations cover every activity that might affect the environment. Consequently every company and every citizen needs to be aware of those rules that affect them.

There are very many books about the environment, environmental protection, and environmental science. Discovering the Earth is different—it is a multivolume set for high school students that tells the stories of how scientists arrived at their present level of understanding. In doing so, this set provides a background, a historical context, to the news reports. Inevitably the stories that the books tell are incomplete. It would be impossible to trace all of the events in the history of each branch of the environmental sciences and recount the lives of all the individual scientists who contributed to them. Instead the books provide a series of snapshots in the form of brief accounts of particular discoveries and of the people who made them. These stories explain the problem that had to be solved, the way it was approached, and, in some cases, the dead ends into which scientists were drawn.

There are seven books in the set that deal with the following topics:

- Earth sciences,
- atmosphere,
- oceans,
- ecology,
- animals,
- plants, and
- exploration.

These topics will be of interest to students of environmental studies, ecology, biology, geography, and geology. Students of the humanities may also enjoy them for the light they shed on the way the scientific aspect of Western culture has developed. The language is not technical, and the text demands no mathematical knowledge. Sidebars are used where necessary to explain a particular concept without interrupting the story. The books are suitable for all high school ages and above, and for people of all ages, students or not, who are interested in how scientists acquired their knowledge of the world about us—how they discovered the Earth.

Research scientists explore the unknown, so their work is like a voyage of discovery, an adventure with an uncertain outcome. The curiosity that drives scientists, the yearning for answers, for explanations of the world about us, is part of what we are. It is what makes us human.

This set will enrich the studies of the high school students for whom the books have been written. The Discovering the Earth series will help science students understand where and when ideas originate in ways that will add depth to their work, and for humanities students it will illuminate certain corners of history and culture they might otherwise overlook. These are worthy objectives, and the books have yet another: They aim to tell entertaining stories about real people and events.

—Michael Allaby
www.michaelallaby.com

# ACKNOWLEDGMENTS

All of the line diagrams and maps in the Discovering the Earth set were drawn by my colleague and friend Richard Garratt. As always, Richard has transformed my very rough sketches into finished artwork of the highest quality, and I am very grateful to him.

When I first planned these books, I prepared for each of them a "shopping list" of photographs I thought would illustrate them. Those lists were passed to another colleague and friend, Tobi Zausner, who found exactly the pictures I felt the books needed. Her hard work, enthusiasm, and understanding of what I was trying to do have enlivened and greatly improved all of the books. Again I am deeply grateful.

Finally, I wish to thank my friends at Facts On File, who have read my text carefully and helped me improve it. I am especially grateful for the patience, good humor, and encouragement of my editor, Frank K. Darmstadt, who unfailingly conceals his exasperation when I am late, laughs at my jokes, and barely flinches when I announce I am off on vacation. At the very start, Frank agreed this set of books would be useful. Without him they would not exist at all.

# INTRODUCTION

*Ecology* is a term on everyone's lips. Hardly a week passes without a newspaper or television report on an event or development as having a good—or more often a bad—"ecological" implication. Commercial products that their makers claim cause no pollution are marketed as being "eco-friendly." Governments enact "eco-friendly" or "eco-unfriendly" laws. What does all this mean?

*Ecology: Plants, Animals, and the Environment* aims to trace the origin of ecology and to explain what it is and how it has developed. In doing so, it becomes clear that *ecology* has two quite distinct meanings. On the one hand, it is the name of a scientific discipline, pursued by patient observation, experiment, and the application of statistical tests to interpret results. On the other hand, it is a shared belief system that inspires a popular environmentalist movement. To an environmentalist, *ecology* refers to the way the natural world once was and how it should be now. It is an ideal for which they believe we all should strive. The two meanings are quite separate, but that does not preclude ecologists from being environmentalists. Many are.

Although the science of ecology emerged recently, it has a long ancestry. The book begins with the story of Gilbert White, the English clergyman whose correspondence describing and commenting on the plants, animals, and events in his rural parish has become a classic. White was an observer, but already there was a long tradition of forest conservation, because trees have always been a major economic resource. It has never made any sense at all to fell trees faster than other trees can grow to replace them. Consequently, tree conservation began a very long time ago.

In 19th-century North America, conservation acquired a new strand: the love of wilderness. The book tells of the early enthusiasts for the American wilderness, and it goes on to relate their concern about what was happening to the wild prairie to the tragedy that led to the dust bowl of the 1930s.

Before the study of natural communities could advance very far, naturalists had to agree on a system for naming and classifying species. The book describes the contribution made by the English naturalist John Ray and also the origin of the classification that biologists use today, invented by the Swedish botanist Carl Linnaeus. As European botanists of the 18th and 19th centuries, including Linnaeus, built vast plant collections from specimens sent to them from all over the world, they learned something of the geography of plant distribution, a study that was pioneered by James Cook, Alexander von Humboldt, and many others. Chapter 4 tells their story.

It was at this stage that naturalists encountered the work of Charles Darwin. Chapter 5 begins by describing Darwin's voyage on HMS *Beagle,* and it explains, briefly, the theory of evolution by means of natural selection. Darwin's theory offered an explanation for how species adapt to the conditions in which they live, and in that way it allowed the study of communities to become much more rigorous. It was Darwin's book that led to the coining, by the German zoologist Ernst Haeckel, of the word *ecology.* The chapter continues with an account of the discovery of the biosphere by the Russian scientist Vladimir Vernadsky, and it tells of James Lovelock and his "Gaia" hypothesis.

Ecology was becoming established, and in chapter 6 the book traces its development, first in aquatic systems, including lakes in North America and Switzerland. Elsewhere the emphasis was different, and European botanists began to classify plant communities. Chapter 7 explains how phytosociology began and how it works.

North American ecologists followed a different path. Chapter 8 describes how they established much of the theoretical principles underlying ecology. The book then turns to the work of their British colleagues, including R. A. Fisher, the mathematician who did much to unify ecology with the study of evolution. That work led to the development of sociobiology, yet another branch of the biological sciences—and a controversial one. Sociobiology is the subject of chapter 10.

The final chapter traces the rise of the modern environmental movement. Modern environmental concern began in the early 1960s with a book: Rachel Carson's *Silent Spring,* which triggered the rise of a large and international popular movement. The first phase of the present environmental movement reached a climax in 1972, with the United Nations Conference on the Human Environment. The book explains how this came about and what the conference achieved. A succession of other UN conferences with relevance to environmental concerns were held during the 1980s, but the book jumps directly to the successor to the 1972 conference, which was held in 1992 in Rio de Janeiro. Finally, the book outlines, very briefly, the progress made so far in improving environmental quality.

Clearly, the subject is vast, and it would be impossible in a single book to do more than provide an impression of its history and scope. For readers whose appetite is whetted, the list of further resources gives details of books and Web sites that open the way to wider and more detailed information.

1

# Gilbert White and His Letters to Naturalists

Modern scientists communicate with one another by e-mail and telephone, and they sometimes attend conferences where they meet colleagues working in the same field. A journey of a few hours by car, train, or air is sufficient to bring people together. This is a very recent development, however. In the days before modern fast transport, and before telephones and e-mails, when people traveled on horseback or by horse-drawn coach and went overseas by sailing ship, journeys were long, uncomfortable, and sometimes dangerous. There was much less travel than there is now, and people communicated mainly by letter instead of meeting face-to-face.

Scholars wrote to one another to describe their work and to debate issues of the day. Some of those letters have survived, and, with the help of his publisher brother, the author of two sets of letters collected them into a book that has never been out of print since it first appeared in 1789. This chapter describes that book, *The Natural History and Antiquities of Selborne,* and its author, Gilbert White (1720–93). White was a close observer of the natural world and of the relationships among species. He never interfered with the plants and animals he described, and he studied them alive and outdoors in their natural habitat, rather than working in a laboratory with dead specimens as most naturalists did. His approach was novel, and it gives White some claim to being the world's first ecologist. *Ecology* is the scientific study of the relationships among living organisms and between living organisms and the living and nonliving components of their environment.

Farms cover most of lowland Britain, and in Gilbert White's day agriculture was the primary economic activity for the people of Selborne, a village in the south of England, as it was for most people. Life was precarious—though there had been no peacetime famine in England since 1623–24, a poor harvest still meant very real hardship. There was a need to find ways of improving crop yields, and one way was to reduce crop losses caused by pests. Yet naturalists such as White enjoy studying the insects, mice, seed-eating birds, and other animals that feed on farm crops and have no desire to see them disappear. This conflict between growers and naturalists continues to the present day, and this chapter ends by describing the way pests have been controlled over the centuries.

## THE NATURAL HISTORY AND ANTIQUITIES OF SELBORNE

Selborne is a village in Hampshire, in southern England. Today its population is about 650 persons, close to what it was in the late 18th century. In the first of the letters that he collected into his book, Gilbert White (see the sidebar on page 3) described the village's location and setting in the following words:

> The parish of Selborne lies in the extreme eastern corner of the county of Hampshire, bordering on the county of Sussex, and not far from the county of Surrey; it is about fifty miles south-west of London, in latitude 51, and near midway between the towns of Alton and Petersfield. . . . The soils of this district are almost as various and diversified as the views and aspects. The high part to the south-west consists of a vast hill of chalk, rising three hundred feet above the village . . . The prospect is bounded to the south-east and east by the vast range of mountains called the Sussex Downs . . .

The Wakes was—and is still—a substantial house, as the 19th-century illustration on page 4 shows. It is now a museum, renamed Gilbert White's House; it also contains material relating to the Oates family, including Captain Lawrence Oates (1880–1912), the Antarctic explorer who died on the Ross Ice Shelf, Antarctica, during

## GILBERT WHITE, NATURALIST OF SELBORNE

Gilbert White was born on July 18, 1720, at The Wakes, the vicarage in Selborne, Hampshire, where his grandfather was the Church of England (Episcopalian) vicar. Gilbert was the eldest of 11 children. His formal education began at a school in Basingstoke, a Hampshire town about 15 miles (24 km) from Selborne, where his teacher was the Rev. Thomas Warton (1688–1745), the father of Thomas Warton (1728–90), a famous poet. In 1740 White entered Oriel College, University of Oxford, where he graduated in divinity in 1743. He was elected a fellow of Oriel College in 1744 and remained one until his death, but he lived there for only his first, probationary year until 1752–53, when he lived in the college while he served as junior proctor of the university. (At the Universities of Oxford and Cambridge, senior and junior proctors are university officers, elected for one year, who perform certain duties, including supervising student examinations and imposing discipline on students.) He became dean (the clergyman who officiates at college services) of Oriel College in 1752, and in 1757 White was a candidate for the post of provost (college head) of Oriel, but failed to be elected.

White was ordained as a deacon in 1746 and fully ordained in 1749. In 1747 he became a curate (an assistant to a parish priest or a priest who takes charge of a parish during the absence of the incumbent) at Swarraton, Hampshire. In 1751 he was appointed curate at Selborne, but left in 1752 to take up the junior proctorship at Oxford. He became curate at Durley, Hampshire, in 1753, and in 1757 he became curate at Moreton Pinkney, Northamptonshire, although he never lived in the parish. He was also curate in Newton Valence and in 1761 at Farringdon, both close to Selborne, and in Selborne itself on two more occasions. On the death of his father in 1758, White move into The Wakes. He inherited the house in 1763.

In 1784 he left Farringdon to become curate of Selborne for the fourth time and remained in this position for the rest of his life. The vicar of the parish of Selborne was appointed by Magdalen College, Oxford. White had studied at Oriel and consequently was ineligible to become vicar of Selborne.

Gilbert White never married, and apart from smallpox, from which he fully recovered, he suffered no serious illness. He traveled, but only in southern England and as far north as Northamptonshire, in the English Midlands. He spent all of his time engaged in his pastoral duties, tending his garden, walking in the countryside, keeping meticulous notes of his observations and experiences, and corresponding with friends and other naturalists. He died at Selborne on June 26, 1793.

the ill-fated expedition led by Robert Falcon Scott (1868–1912). The museum attracts about 30,000 visitors a year.

An enthusiastic and careful gardener, White was also highly observant and began noting the wildlife that appeared in his garden. When not gardening or busy with pastoral duties, he would take long

"The Wakes" in the village of Selborne, where Gilbert White (1720–93) was born, lived throughout his working life, and died *(Topham/The Image Works)*

walks in the countryside around Selborne. There, too, he observed the wild plants and animals. For a short time Stephen Hales (1677–1761) was rector of the parish of Farringdon, near Selborne, and it is likely that the two men were acquainted. Hales, a fellow of the Royal Society, had studied the movement of water through plants and of the blood circulation in animals, and as an eminent physiologist, chemist, and inventor he would certainly have appreciated White's meticulous attention to detail. It may have been Hales who, in 1751, suggested to White that he keep a journal in which he recorded his observations. At first, White's journal recorded events in his garden. This grew into *Calendar of Flora and the Garden,* published in 1765, and in 1768 it changed its form, becoming *The Naturalist's Journal,* in which White described the plants and animals around Selborne.

*The Naturalist's Journal* followed a style and format designed by Daines Barrington (1727–1800), who sent White a book of that type. The two men met in London in 1769 and became close friends. Barrington was a lawyer, antiquary, and naturalist, and fellow of the Royal Society. They began a correspondence that continued for 14 years. White also corresponded with Welsh naturalist and antiquary Thomas Pennant (1726–98), who was then the leading British zoologist. White's letters (numbered in the published book) were replies to inquiries from Baines and Pennant, but in the form of detailed accounts of familiar plants and animals and, most important from a modern point of view, the relationships between them and the behavior of animals. His observations were acute. In Letter II to Barrington, for example, dated November 2, 1769, White notes that: "All birds that continue in full song till after Midsummer appear to me to breed more than once." In Letter XI to Pennant, dated September 9, 1767, White made the following observation about bats:

> I was much entertained last summer with a tame bat, which would take flies out of a person's hand. If you gave it anything to eat, it brought its wings round before the mouth, hovering and hiding its head in the manner of birds of prey when they feed. . . . Insects seem to be the most acceptable, though it did not refuse raw flesh when offered: so that the notion that bats go down chimnies (*sic*) and gnaw men's bacon, seems no improbable story. While I amused myself with this wonderful quadruped, I saw it several times confute the vulgar opinion, that bats when down on a flat surface cannot get on the wing again, by rising with great ease from the floor.

This linking of species and the ways in which they relate to their surroundings set White apart from earlier natural history writers, who simply described the appearance of plants and animals. White was possibly the first modern writer on natural history, and a century later his approach led to the emergence of ecology as a scientific discipline. He related plants to climate, for example in the following excerpt from Letter XXIX of February 7, 1776, to Pennant:

> Trees perspire profusely, condense largely, and check evaporation so much, that woods are always moist: no wonder therefore that they contribute much to pools and streams.

> That trees are great promoters of lakes and rivers appears from a well-known fact in North America: for, since the woods and forests have been grubbed and cleared, all bodies of water are much diminished; so that some streams, that were very considerable a century ago, will not now drive a common mill. Besides, most woodlands, forests, and chases with us abound with pools and morasses; no doubt for the reason given above.

(Note: a *chase* is a formerly royal forest that has passed into private ownership.)

White could identify birds by their song, and in this way he was one of the first naturalists to differentiate between three British birds that are almost identical in appearance: the chiffchaff (*Phylloscopus collybita*), willow warbler (*P. trochilus*), and wood warbler (*P. sibilatrix*). Between 1768 and 1793, White noted the dates of emergence of more than 400 plant and animal species around Selborne, and the naturalist William Markwick (1739–1813) did the same in Sussex. Emergence dates vary according to the weather conditions, so a long record of them is of great value in reconstructing past climates. Maintaining such records is called *phenology,* and White and Markwick were among the earliest practitioners.

Despite living for so many years in what might appear to be rural isolation, Gilbert White had wide contacts, and Pennant and Barrington were not his only correspondents. Gilbert's eldest brother, Thomas (1724–97) was a scientist and fellow of the Royal Society, and Benjamin (1725–94), the next oldest, was a publisher of most of the works on natural history that appeared during his lifetime. Benjamin introduced Gilbert to both Pennant and Barrington. Gilbert's sister Anne married Thomas Barker, who kept weather records and who inspired Gilbert to do the same, and their son Samuel Barker also became one of White's regular correspondents.

White had a particular interest in swallows (*Hirundo rustica*) and house martins (*Delichon urbica*). These are migratory birds, but in White's day many naturalists doubted that such small birds could fly the long distances migration implied and suggested that they hibernate. White wrote several papers on these birds and in 1774 submitted them to the Royal Society, where they were well received. This encouraged him to consider seriously a suggestion Barrington had made in 1770, that he should publish the letters he had written to Barrington and Pennant. In 1771 White sent Pennant an outline for "a natural history of my native parish, an *annus historico-naturalis* (natural history year), comprising a journal for a whole year, and illustrated with large notes and observations." White thought this might encourage other naturalists to keep detailed records of events in their immediate neighborhood. However, it was 1789 before White's *Natural History and Antiquities of Selborne* appeared. The book was an immediate success.

The book consists of 44 letters to Pennant and 66 to Barrington. As well as comments on plants and animals, White wrote about the weather, with a table of the annual rainfall over several years, the size of the Selborne population (676 in 1783), and the number of male and female baptisms and burials (980 baptisms and 640 burials over the course of 60 years). Although White did some editing of his material, the book is a fairly haphazard compilation. White intersperses anecdotes with the serious observations and records, mentions numbers of species seen but fails to list them, and often digresses. Combined with the direct and personal tone of the letters, the result is charming. White's book is also one of the earliest works on ecology, recording as it does its author's observations of the way plants and animals live and interact with their surroundings.

## CONTROLLING PESTS TO IMPROVE CROP YIELDS

There is an old saying among English cereal farmers:

> Four to sow and two to grow;
> One for the farmer, one for the crow.

There are several versions of the saying, but the message is always the same: Only half of the seeds that a farmer sows will germinate, and pests (in this example the crow) are expected to take half of those, so the farmer can expect to harvest a crop from no more than one-quarter of the seeds he sows. The skylark (*Alauda arvensis*), now becoming rare in Britain, nests on the ground and from time to time rises vertically into the air, climbing high and singing loudly. It is greatly loved by naturalists, but it feeds on sprouting grain, and in the 19th century it was regarded as a pest. Farmers trapped skylarks and sold them for food. London markets often displayed up to 30,000 of these birds for sale to the city's cooks, who would serve them to their wealthy employers. Farmers who did not trap skylarks employed boys to scare them with clappers and rattles. The expansion of arable farming in the 18th century also encouraged an explosion in the population of wood pigeons (*Columba oenas*), which also feed on grain. In Scotland, the East Lothian Agricultural Society offered a bounty of one penny (0.4 pence in modern British money and equal to about 0.6 U.S. cents) for every wood pigeon killed, and between December 1862 and June 1870 it paid for 130,444 birds.

Many birds feed on seeds. When farmers sow seeds, there are birds that take advantage of the abundance of food. The same species appear again later in the year, when grain crops ripen, to take the seeds at the head of each stalk. Pigeons are such heavy birds that simply by flapping their wings as they descend onto the crop they can dislodge very ripe grain from the ears. Mice and other small animals feed on spilled grain, and some will climb the stalks to reach the ears.

Other birds are predators; they hunt smaller birds. This might seem to help the farmer, but small birds are often edible delicacies, and landowners can charge hunters for the right to shoot them. This is a useful source of income, so the birds of prey also compete with the landowner, and they have been heavily persecuted.

Early naturalists, including Gilbert White, were unsentimental about species that compete with humans for food, and especially about insect pests. In his Letter XXXIV to Thomas Pennant, dated March 30, 1771, he suggested that "A full history of noxious insects hurtful in the field, garden, and house, suggesting all the known and likely means of destroying them, would be allowed by the public to be a most useful and important work." No such book existed, but the war against insect pests began a very long time ago, usually using poisons but occasionally employing subtler biological methods. In about 1200 B.C.E. Chinese growers used predatory ants to protect their citrus trees from wood-boring insects. They fastened bamboo sticks or ropes between the trees in their orchards to allow the ants to move easily from tree to tree. Most attempts at pest control relied on chemicals, however. Sumerian farmers were using sulfur compounds against pests in about 2500 B.C.E., and by 100 C.E. the Chinese had discovered that soapy water kills insects.

The problem was—and still is—very real. Aphids, for instance, can devastate a crop, partly by robbing it of nutrients but mainly by transmitting diseases. There are about 4,400 species of aphids, of which about 250 species, also known as plant lice, are serious agricultural and forestry pests. Aphids are soft-bodied insects that range in size from 0.04 to 0.4 inch (1–10 mm) and most species, but not all, feed exclusively on one type of plant. Aphids pierce the plant stem, and when their mouthparts penetrate a *phloem vessel*—phloem vessels transport sugars made by *photosynthesis* to all parts of the plant—the pressure in the vessel forces sap into the insect. This may not seriously harm the plant, but the aphid may infect it with a potentially lethal disease. Aphids need to feed voraciously because plant sap contains very little protein, so to obtain the protein their bodies need the insects consume large amounts of sap and excrete the surplus sugar as a sticky liquid called honeydew.

Aphids are able to infest plants because of their method of reproduction. In pest aphid species, eggs laid in the autumn overwinter in the soil and hatch in the spring, producing only female insects. These females are able to produce female offspring by *parthenogenesis*—development of an egg without fertilization by a male. Each daughter is also able to reproduce in the same way, and it sometimes happens that an aphid produces an offspring before she has emerged from her mother. Where food is abundant the aphid population can increase very rapidly to take advantage of it. The illustration on page 10 shows a colony of one species, the black bean aphid (*Aphis sambuci*) on a plant stem. All the insects in the picture are sisters. In late summer, the changing day length and falling temperature cause the aphids to produce sexual males and females. These mate, lay eggs in the soil, and die.

Modern growers use a variety of techniques to control insect infestations, and they must be very careful in the use of chemicals to avoid harming species that are not pests and may be beneficial to the grower. The use of chemicals is not new, however, and some of the chemicals used in the past were very powerful. By the 17th century, the principal substances used included nicotine and arsenic. Nicotine was obtained by soaking tobacco leaves in water, and the liquor was used against pests on fruit trees. Nicotine was also the only substance that was effective against aphids. It poisons insects on contact, but vaporizes quickly, so plants treated with it are safe to eat a few days later.

Black bean aphids (*Aphis sambuci*) feeding on the stem of a crop plant
*(Dr. Jeremy Burgess/Science Photo Library)*

By the middle of the 19th century several arsenic compounds were in use, and in 1867 a compound known as Paris green, containing copper arsenate, was used successfully to control Colorado potato beetle (*Leptinotarsa decemlineata*) in the eastern United States. Many of the arsenic-based compounds had to be abandoned, however, either because of their danger to humans or because they were poisonous to the plants they were meant to protect.

Cyanide was also used, usually in the form of hydrocyanic gas (HCN). The gas was blown into buildings to fumigate them in order to kill bedbugs and wood-boring insects. From 1886 cyanide was widely used in California against the cottony cushion scale insect (*Icerya purchasi*), which attacked citrus trees. Growers placed tents over the infested trees and pumped in high concentrations of cyanide. Somewhat hazardous for the operators, the method was successful for a time, but then the insects became increasingly resistant to the poison.

Arsenic, cyanide, and nicotine kill indiscriminately. They were replaced in the 20th century by organic compounds that were more specific in their effects, but then new problems emerged. Pesticides that were designed to retain their toxicity, allowing for less frequent applications, lodged in the bodies of invertebrates, and when predators ate those invertebrates the compounds accumulated in the predators' bodies. Eventually they reached concentrations that were high enough to cause harm, generally by reducing the ability of species to reproduce successfully.

Food production and commercial forestry modify the natural environment. Farmed landscapes can be very attractive, but they are very far from being natural, and if farming and forestry were abandoned, within a few years other types of vegetation would colonize the land. Naturalists, and more recently conservationists, recognized the extent of this modification and its inevitability, but over the years they have sought to minimize its adverse effects on the wild plants and animals the farmers and foresters had displaced.

2

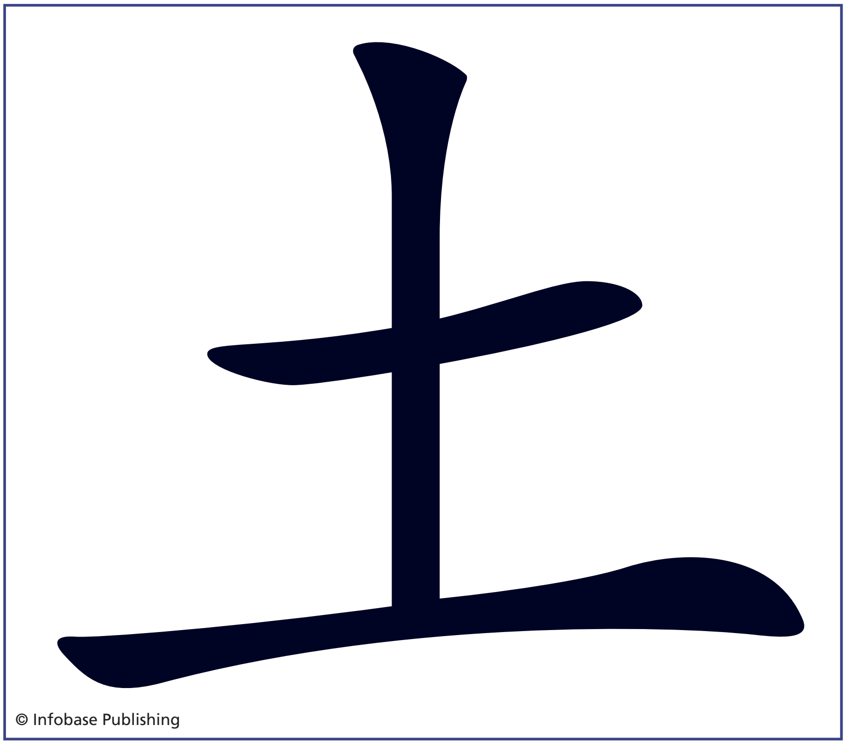
# The Beginning of Conservation

Modern conservationists seek to protect wild plants and animals for their own sake, because nonhuman species have a right to exist and because they enrich our own lives. This is true even of species most people will never see in the wild. Few Americans or Europeans will be fortunate enough to see giant pandas in their bamboo forests or gorillas in their tropical forests. Nevertheless, everyone can enjoy seeing these animals on film, knowing that it is at least possible to travel to the regions where they live and to see them there. The extinction of such animals would diminish everyone.

While concern for the natural world is not new, its motivation has changed. For most of history, people were deeply integrated into their natural surroundings. They depended on it for building materials, fuel, food, and fibers, and it was obvious that if these essential resources were overexploited, eventually there would be an insufficient number of them for everyone's needs. There would be shortages, leading perhaps to the need to leave the area and find somewhere else to live. This close relationship is reflected in some of the characters in which Chinese languages are written. The two illustrations (on pages 13 and 14) are good examples. The character for soil consists of two horizontal strokes and one vertical stroke. The scholar Xushen (58–147 C.E.) noted that the lower horizontal stroke might refer to the subsoil, the upper horizontal stroke to the topsoil, and the vertical stroke to a plant growing in the soil. The character for *earth* has two parts. On the left is the character for *soil.* The part on the right is the character for *also.* So together their literal meaning is soil also, or soil extended over a vast area.

There are parts of the world where people still live in this intimate association with wildlife. In India, for instance, approximately 360 million people—one-third of the population—live in or very close to the forests. More than half of these people live below the official poverty line, and consequently they depend crucially on the resources they obtain from the forests. The Indian government now runs programs aimed at improving their lot by involving them in the commercial management of their forests, in this way allowing them to continue to obtain the food and materials they need, but at the same time to sell forest produce. If the programs succeed, forest dwellers will be more prosperous, but they will be able to preserve their traditional way of life and culture, and the forest will be managed sustainably, so the wildlife is not depleted.

Although the Indian example is happening now, the recognition of the need to manage essential materials in a sustainable fashion




The Chinese character for *soil* is composed of a long base stroke, perhaps representing subsoil; a shorter upper stroke, perhaps indicating topsoil; and a vertical stroke, perhaps representing a growing plant.


The Chinese character for *earth* consists of two parts—on the left is the character for *soil* and on the right that which means "also." The literal meaning, therefore, is "soil also."

is ancient. The kings of Assyria, a country located in what is now northern Iraq, loved to hunt wild animals, especially large ones such as lions, elephants, ostriches, and bulls. The hunts had symbolic value. By succeeding in the hunt, the king demonstrated that the gods favored him; this proved that his rule was legitimate. The hunt itself was a highly ritualized public spectacle. The animal was released from a wooden cage and driven toward the king, who usually shot it with bow and arrow while standing in his chariot. He poured wine over the animal he had just killed and made a speech attributing his success to the goddess who watched over him. Pictures of royal hunts decorated many walls in Assyrian palaces, and written accounts are preserved on clay tablets. The animals for the hunt were captured, some as far away as Africa, and brought to Assyria, where they were held in a game reserve until they were needed. The game reserve was a royal hunting forest in which the natural environment was protected. Decrees establishing them date from 700 B.C.E.

The Chinese were also aware of the need to conserve resources. *Science and Civilization in China* consists of seven volumes written by Joseph Needham (1900–95), publication of which began in 1954 and still continues. Many scholars recognize this work as one of the most authoritative accounts of its subject. In it Needham reported that the philosopher Mencius (Mengzi or Meng Tsu, 371–289 B.C.E.) likened deforestation to the forcible debauchery of the natural goodness inherent in the human race. Needham also quotes the following advice, which sounds very modern, from the *Mengzi* (*Book of Mencius*), written in about 120 B.C.E., long after Mencius's death:

> If the seasons of husbandry be not interfered with, the grain will be more than can be eaten. If close-mesh nets are prohibited in the pools and lakes, the fishes and turtles will be more than can be consumed. If axes and hatchets are used in the mountain forests only at suitable times, there will be more wood than people know what to do with.

This chapter outlines the origin of conservation and the sustainable exploitation of natural resources in Europe and North America. It begins in medieval England, where the allocation of resources was enshrined in ancient custom, reinforced by the law. It continues by describing the origin and development of forestry in the 17th century and the growing awareness of the dangers of unregulated deforestation in the United States in the 19th century. This awareness led to the formation of the first national parks and wildlife reserves and to the appreciation of wilderness, exemplified in the writing of Henry David Thoreau (1817–62) and Aldo Leopold (1887–1948).

The chapter then explores the causes of the drought that afflicted the Great Plains in the 1930s and produced the dust bowl. That tragedy was due partly to the unwise use of land, and the chapter ends with a discussion of "The Tragedy of the Commons," which was a very famous essay on the topic of resource use.

## RENEWABLE RESOURCES IN MEDIEVAL FORESTS

Robin Hood and his merry men have entertained people for many centuries. The name Robin Hood first appears in texts written in the early 13th century, but Robin (a diminutive of Robert) was a common given name in medieval England, and Hood, originally referring to the head covering that most men wore, was also a common name. So there were many genuine Robin Hoods, and the first undoubted references to the legendary hero date from early in the 15th century. The very first reference locates Robin in Sherwood Forest, near Nottingham in the North Midlands. Another, written in 1420, locates Robin and Little John in Inglewood Forest, in Cumbria, in northwestern England.

Although no one knows whether or not the literary character is based upon a real person, the message of the stories is clear. Robin and his band were outlaws, living beyond the reach of the law and, in most of the stories, spending much of their time outwitting the wicked but utterly incompetent sheriff of Nottingham. The outlaws lived off game that they hunted, and they robbed wealthy individuals passing through the forest, distributing the proceeds to the oppressed poor.

In medieval England, kings and aristocrats ate mainly venison, which was obtained by hunting wild deer. The deer lived in protected areas called forests—whether or not they were wooded. A forest, from the Latin *foris* meaning outside, was an area subject to special laws. Kings and their courts did hunt for sport, but this did not occupy very much of their time, and they enjoyed many other games and entertainments. The forests were managed as a source of food, and the royal court moved around the country, essentially from forest to forest. The forest resources, especially the deer, were protected by laws administered through special courts by justices, wardens, foresters, and a hierarchy of other officials under the overall control of the king or his sheriff. The officials collected fees and were entitled to use certain of the resources, including the right to pasture livestock and obtain timber and small wood. They also made money from the local population in many other unofficial ways. The entire system fostered corruption, and it aroused much popular resentment. It is that resentment which the Robin Hood stories record.

The forest courts spent most of their time charging fines. Offenders were sometimes fined, but most fines were raised to provide income for the officials. They were the equivalent of taxes, rents, and the sale of certain rights. Even people who stole deer were not treated harshly, despite the fact that the deer belonged to the king.

The thief usually received a fine and a short term of imprisonment. An individual who appropriated an area of forest for private use committed the offense of *assart,* but was often allowed to keep the land on payment of a rent. Forests also provided kings and other landowners with an inexpensive way to reward their friends and secure the allegiance of nobles and institutions. They could give away venison, other forest resources, and even areas of forest. This practice became so widespread that in 1257 it was suspended in many forests because of the damage it caused. A letter has survived that was written in the middle of the 12th century by a bishop in Norwich, in eastern England, rebuking his *woodward*—a forest keeper in charge of the growing timber—for giving away wood in this way. "I appointed you custodian of the Wood," he scolded, "not the rooter up of it . . . Guard the Wood of the Holy Trinity, as you wish to be guarded by the Holy Trinity, and to continue in my favor."

Forest managers recognized the need to conserve the living resources of the forest, and even if they were not imposed stringently or consistently, there were severe restrictions on what ordinary people were allowed to do. People living in the forest were not allowed to cut down trees, even on their own land, far less to remove the trees altogether. Often they were not allowed even to collect dead wood.

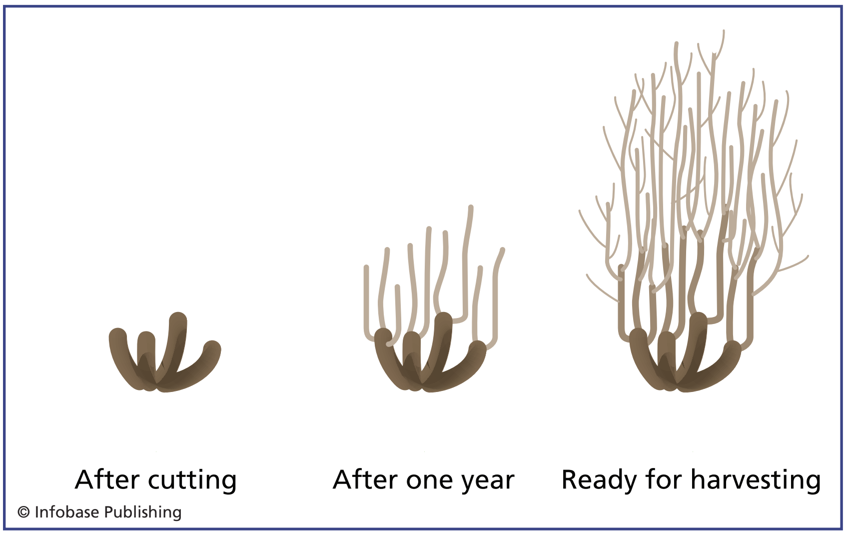
By the middle of the 13th century, the principle underlying English woodland management was that when a tree was felled another tree should replace it. This usually involved allowing a young sapling to grow to full size. However, English building tradition did not call for many large pieces of timber—English buildings, including large buildings such as churches, were constructed by a method introduced by the Anglo-Saxons. The building was made from a frame of upright posts, strengthened by horizontal struts, with the spaces filled with wattle and daub—small pieces of wood held together by mud—and painted to make it weatherproof. Bricks were later used in place of wattle and daub. This produced the attractive "half-timbered" buildings so typical of many parts of northern Europe—the technique is called *Fachwerk* in Germany, where it is still used. Builders required poles of a range of sizes, rather than whole tree trunks, and the wood did not have to be precisely straight because the infilling technique could accommodate irregular shapes. *Coppicing*—cutting trees close to or just below ground level to stimulate the growth of many poles—

produced wood of this kind. No one knows when coppicing was first practiced, but trackways in the Somerset Levels, in the west of England, constructed during the Neolithic period (2500–2200 B.C.E.), are made from hazel and ash poles laid across the marsh; these were most likely produced by coppicing. Certainly the technique was well established in England by the 11th century, and by the middle of the 13th century it was widespread.

Coppicing is the technique of cutting through a tree either just above or just below ground level. This fells the tree, obviously, and if the tree is a conifer such as a pine, spruce, larch, fir, or hemlock, in most cases it will kill it. But most broad-leaved species do not die. Instead, the tree produces new shoots from around the edge of the stump. These grow rapidly into poles. The diagram below shows the sequence. Some willows (*Salix* species) have been known to grow 11 feet (3.3 m) in their first summer and oaks (*Quercus* species) cut down in spring may produce poles seven feet (2 m) tall and one inch (2.5 cm) thick by autumn. When the poles are of a useful size, they are cut, and the tree produces another crop. Far from injuring the tree, in most cases coppicing extends its life.

Different tree species grow at different rates. Hazel (*Corylus* species) takes about seven years to produce useful poles; chestnut (*Castanea* species) takes between 15 and 20 years. An area of forest that was to be coppiced would be divided into small areas, the number of areas depending on the tree species; multiples of 15–20 for chestnut, for instance, and multiples of seven for hazel. If the crop was hazel, for example, and there were 35 small areas (= 7 × 5), then five areas would be cut in year one, another five in year two, and so on until year eight, by which time the first crop of poles would be ready in the areas cut in year one. Every year after that, five of the areas

Coppicing is a traditional management technique for producing long, thin poles. The tree is cut close to the ground (or to just below ground level). It then produces shoots from the cambium tissue in the inner bark. These grow until they are of suitable size.



would produce a crop of poles. Medieval cropping cycles varied widely, however, depending on local circumstances and variations in demand. Some cycles were as short as four years, while many allowed seven years between harvests. Each time trees or poles are cut, the area is left exposed to the light. This encourages plant growth—of the trees and also of many herbs, so the technique is good for wildlife.

Cutting to ground level does kill some broad-leaved trees, including aspens (*Populus* species) and most elms (*Ulmus* species), but these produce new shoots, called *suckers,* from their roots or the base of the trunk. These emerge around the dead tree, forming a crop of poles that are genetically identical. The clump of poles comprises a *clone.* The clones can be harvested almost indefinitely, as though the trees had been coppiced.

Coppiced woodland had to be fenced to keep out animals that would otherwise bite off the young shoots. Anyone who allowed cattle or sheep into coppiced woodland would be fined. *Pollarding* was an alternative technique, however, that allowed the land to be grazed. It involved cutting through the tree about seven feet (2 m) above ground level. The tree produced a crop of poles, but these were out of the reach of farm livestock.

Large trees were also required, of course, to produce long, straight timber. In medieval England, oaks (*Quercus robur* and *Q. petraea*) were often allowed to grow to their full size, producing woodlands where tall trees stood among coppiced trees, a technique known as coppice-with-standards. Those who were to use the timber, such as builders, architects, and shipbuilders, walked through the forest and chose their trees for size and shape. The selected trees were then felled to order—and the same number of saplings was allowed to grow up to take their place.

## JOHN EVELYN AND FORESTRY

Landowners had deliberately planted trees in England at least since Anglo-Saxon times. They planted individual trees to fill gaps in their forests, and they planted orchards to provide a regular supply of fruit. They were not planting areas of land with trees for timber or coppice production, but that was beginning to happen elsewhere in Europe.

Medieval German farmers used to plant oaks around their farmsteads to provide acorns to feed pigs, bark for tanning leather, and after a few generations the trees supplied construction timber. This practice expanded in the 13th century to the planting of trees, mainly oak, in order to replace the forest in areas that had been clear-felled. There are records of oak plantations of this kind in 1343 near Dortmund, on the Dresden Heath in 1357, and in the City Forest of Frankfurt in 1398. In 1368 several hundred acres in the Lorenzer Forest near Nuremberg were planted with Scots pine (*Pinus sylvestris*). That is the first record of a conifer plantation, and over subsequent centuries the practice expanded, replacing much of Germany's native broad-leaved forests, consisting mainly of oak and beech, with plantations of pine, spruce, or fir.

The idea of planting entire forests developed later in Britain. Some small plantations were probably established in Scotland around 1500, and in 1580 Queen Elizabeth I ordered the planting of oaks in Windsor Great Park. The park was a royal forest that had been greatly depleted by felling to provide timber for construction and shipbuilding, and the queen's chief minister, William Cecil (1520–98), who later became Baron Burghley, organized the planting. It was the first recorded plantation of oaks in England—and some of the trees are still standing.

It seems like common sense to plant species of trees that will produce valuable timber and small wood, but the first enthusiast for large-scale tree planting was John Evelyn (1620–1706). Evelyn was born on October 31, 1620, at Wotton House, near Guildford, Surrey, into a landowning family that had amassed a considerable fortune from manufacturing gunpowder. When he was five years old, Evelyn went to live with his mother's parents at Cliffe, near Lewes, Sussex. He refused to go to school at Eton College, but when his grandmother remarried following his grandfather's death and moved to nearby Southover, Evelyn went to school there. In February 1637 he entered the Middle Temple, London, to study law, and in May of the same year he entered Balliol College, University of Oxford. He left university without taking a degree, and in 1640 he was living in Middle Temple. His father died in that year, and in July 1641 Evelyn crossed to the Netherlands, where he joined a company in King Charles I's army. He returned to England after six days' training, arriving just before the outbreak of the Civil War. He left the army and returned to Wotton, but in 1643 he left once more, visiting cities in France and Italy, then in 1646 returning to Paris, where he became friendly with Sir Richard Browne (1605–82 or 83), the English resident at the French court. In June 1647 he married Browne's daughter and heiress, Mary, who was then only 12 years old (her date of birth is not known). He then returned to England, leaving his wife in the care of her parents. Evelyn maintained a correspondence with his father-in-law, written in code and concerning Royalist matters, and in 1649 he moved back to Paris. When Charles II (1630–85) was defeated at the battle of Worcester in 1651, Evelyn became convinced that the Royalist cause was lost. In 1652 he finally settled in England, moving into Sayes Court, at Deptford (now a district of London). Sir Richard Browne held the house on a lease from the Crown. The Parliamentarians had seized it, but allowed Evelyn to rent it, and following the Restoration of the monarchy in 1660, Evelyn became the owner. His wife joined him there, and their first son, Richard, was born there in 1652.

During the Commonwealth period, Evelyn occupied himself mainly with gardening and making friends among the leading scientists of the day, but he also maintained a coded correspondence with the king. After the Restoration, he was one of the group of intellectuals who formed the society that the king's charter of 1662 made into the Royal Society; the charter named Evelyn as a member of its council. From that time until his death, Evelyn remained in favor at the royal court, which he visited frequently, but he never held any high public office.

John Evelyn died at his home in Deptford on February 27, 1706. His wife, Mary, died in 1709. The couple had eight children, seven of whom predeceased them: Richard (1652–58), John Standsfield (1653–54), John (1655–99), George (1657–58), Richard (born 1664 and died the same year), Mary (1665–85), Elizabeth (1667–85), and Susanna (1669–1754).

Evelyn is remembered as a diarist and as the author of two famous works. The first was a pamphlet published in London in 1661, with the title: *Fumifugium, or, the inconvenience of the aer and smoak of London dissipated with some remedies humbly proposed by J. E. esq. to His Sacred Majestie, and to the Parliament now assembled.* It is one of the very first written comments on air pollution. Evelyn also recommended a novel fuel that he claimed was smokeless, made from charcoal dust mixed with loam. He described it as "very glowing, and without smoke or ill smell."

His other work, first published in full in 1664, was *Sylva, or A Discourse on Forest Trees, and the Propagation of Timber in His Majesties Dominions.* Evelyn knew a great deal about trees and their cultivation. The commissioners of the Royal Navy had sought his advice on this, and on October 15, 1662, Evelyn noted in his diary that "I this day delivered my *Discourse concerning Forest-Trees* to the Society, upon occasion of certain queries sent to us by the Commissioners of his Majesty's Navy, being the first book that was printed by order of the Society." On November 5 Evelyn mentions a meeting held at the end of a Royal Society council meeting "where was a discourse suggested by me, concerning planting his Majesty's Forest of Dean with oak, now so much exhausted of the choicest ship-timber in the world." This led in 1688 to a major program of planting in the Forest of Dean, in Gloucestershire. The *Discourse—Sylva*—was well received by the members of the Royal Society.

*Sylva* had three parts. The first contained instructions for growing apples for cider—in Britain cider is an alcoholic beverage made by fermenting apple juice. The second part was a general gardening manual. The third part of the book was the most important. It described in practical detail the cultivation of different species of trees and the uses for their timber. Among other topics, the book explained pruning, the control of insect pests, the treatment of wounds, and transplanting. *Sylva* was written for landowners, and Evelyn's aim was to encourage them to establish forest plantations that would ensure a continuing supply of good-quality timber. The book immediately became a best seller, and for the next 150 years it was the standard instruction manual for plantation forestry. A second edition appeared in 1670, a third with an added section about soils in 1679, and a fourth edition in 1706 that was enlarged still further by the addition of a section on growing salad crops. More editions appeared in subsequent years, some of them consisting of the forestry section by itself. The last edition appeared in 1825.

Impressed by Evelyn's work, during the latter part of the 17th century landowners began establishing tree plantations. At first most were small and were coppiced, but as time passed, the area of plantation increased, and what had started as a hobby for the wealthy developed into a profitable business. At some time in the 19th century, the area of plantation forests in Britain overtook the area of natural forest, and as the plantations expanded, they came to include more imported tree species. Finally, the plantations achieved the form they had through the 20th century, of forests grown for timber production, consisting of a small number of species, often just two or three conifers. Plantations had begun as replicas of natural forest. They became an entirely different form of land use. Today they are slowly changing back. As the conifer plantations mature and are felled, it is forestry policy to replace them with a mixture of species, so far as possible self-sown native trees. Large amenity forests are also being planted, and these also consist of native broad-leaved species. In the course of the 21st century, British plantation forests will come increasingly to resemble the country's original natural forests.

## GEORGE PERKINS MARSH AND THE CONSEQUENCES OF DEFORESTATION

John Evelyn and the commissioners of the Royal Navy were worried that in years to come British forests would be unable to supply a sufficient quantity of the tall, strong trees that were needed to build the ships to defend the nation's interests, and especially its trade routes. It is possible that their anxiety was misdirected and that trees of the requisite quality were plentiful, but the commissioners were unwilling to pay the realistic market price for them, so landowners refused to sell. Be that as it may, the adverse environmental consequences of extensive deforestation were more serious.

Plato (428 or 427–348 or 347 B.C.E.), the Greek philosopher, wrote a number of dialogues in which various characters debated matters of interest. The titles of the dialogues were the names of the principal speakers. In the *Critias,* written in about 360 B.C.E. (and one of the dialogues that mentions Atlantis), Critias tells how deforestation brought about soil erosion and ruined the land around Athens. "The earth has fallen away all round," Critias said, "and sunk out of sight. The consequence is, that in comparison of what then was, there are remaining only the bones of the wasted body . . . the mere skeleton of the land being left. But in the primitive state of the country, its mountains were high hills covered with soil, and the plains . . . were full of rich earth, and there was abundance of wood in the mountains."

In the early 19th century, North America, a continent of vast forests, seemingly endless grasslands, wide rivers, huge lakes, and majestic mountains, appeared to offer limitless resources. Geographers and *geomorphologists*—scientists who study landforms and their origins—had no doubt that the landscapes they saw before them were the result of the physical forces of nature, principally of temperature, wind, rain, snow, and ice. Americans depended greatly on timber from the forests for building, making furniture and other articles, and as fuel, and the demand for fuel increased rapidly with the expansion of the railroads and their wood-fired locomotives. People assumed that if they felled trees—no matter how many—more trees would spring up to take their place. Few Americans had seen for themselves the evidence from southern Europe that might challenge their view. One who did see that evidence—and understood its meaning—was a U.S. diplomat, George Perkins Marsh (1801–82). In 1849 President Zachary Taylor (1784–1850) had appointed Marsh U.S. minister resident in Turkey, and Marsh represented his country on a diplomatic mission to Greece in 1852–53. In 1861 President Abraham Lincoln (1809–65) appointed him to be the first U.S. ambassador to the newly formed kingdom of Italy.

Marsh had a brilliant mind and a keen eye. As he traveled through Italy, Greece, and Turkey, he saw badly eroded land where his extensive reading of European history and literature told him there had once been fertile plains and forested hills. He read that in ancient times the hills had been stripped of their forests, leaving the soil exposed to the heat of the Mediterranean summer and rain and winds of the winter, and he saw the result. Over the centuries, the bare soil had been eroded, greatly impoverishing the farmers and peasants who in his day toiled to scrape a meager living from the land. Marsh recognized in the Mediterranean landscapes the end product of the deforestation and soil erosion he had seen as a child near his home in Vermont.

His observations and reflections stimulated him to write a book that would warn Americans of the long-lasting damage that deforestation could cause. In 1864 he published *Man and Nature; or, Physical Geography as Modified by Human Action*. For the second edition, published in 1874, Marsh changed the title to *The Earth as Modified by Human Action: Man and Nature*. The book was well received by critics and by scientists, was read widely by the general public, and Marsh's clear message was taken to heart. *Man and Nature* led directly to the establishment of the U.S. national forest system in 1891 and of forest reserves, and it stimulated various forest conservation measures in other countries.

In *Man and Nature,* Marsh made a sharp distinction between natural changes to the environment and those brought about by human activities. He was by no means a preservationist, seeking to protect forests from any commercial exploitation. His message was that humans, uniquely in nature, have the capacity to cause serious harm. He urged the restoration of what would now be called degraded land and that new developments should not proceed until, so far as is possible, their full environmental effects had been determined. The following two short passages from *Man and Nature* encapsulate Marsh's view:

> [Passage one] Man has too long forgotten that the earth was given to him for usufruct alone, not for consumption, still less for profligate waste. Nature has provided against the absolute destruction of any of her elementary matter, the raw material of her works; the thunderbolt and the tornado, the most convulsive throes of even the volcano and the earthquake, being only phenomena of decomposition and recomposition. But she has left it within the power of man irreparably to derange the combinations of inorganic matter and of organic life, which through the night of aeons she had been proportioning and balancing, to prepare the earth for his habitation, when, in the fullness of time, his Creator should call him forth to enter into its possession.

> [Passage two] We are, even now, breaking up the floor and wainscoting and doors and window frames of our dwelling, for fuel to warm our bodies and seethe our pottage, and the world cannot afford to wait till the slow and sure progress of exact science has taught it a better economy. Many practical lessons have been learned by the common observation of unschooled men; and the teachings of simple experience, on topics where natural philosophy has scarcely yet spoken, are not to be despised.

In *Man and Nature,* Marsh went beyond the study of natural history. He was not observing the behavior of animals or the growth of plants, or compiling catalogs of species as other naturalists had done before him. Marsh, in contrast, was interested in the way species, and especially humans, fit into their immediate environment and how they modify it. He did not quantify his observations or apply statistical tests to identify patterns of cause and effect, but his outlook was that of an ecologist. Although the terms are often used as though they were synonyms, in fact environmentalism is not at all the same thing as the scientific discipline of ecology. Marsh is often called the first environmentalist; he was also one of the first ecologists—before the term had been coined.

George Perkins Marsh was born on March 15, 1801, at Woodstock, Vermont. His father, Charles Marsh, was a successful lawyer, district attorney for Vermont, and formerly a U.S. senator. The family lived in the foothills of the Green Mountains, beside the Ottaquechee River. George Marsh used to climb nearby Mount Tom, from where he could see the main range of the mountains covered by forests of spruce and hemlock, but the hills around Woodstock had been cleared of their forests, mainly for fuel, and converted to fields and pasture. An enthusiasm for study kept him indoors much of the time, however, although his poor eyesight sometimes restricted his reading. His father taught him geography and morals, and his elder brother taught him Latin and Greek. He was sent to Phillips Academy, in Andover, Massachusetts, in 1816, but he was far ahead of the other students, so he left after a few months and moved to Dartmouth College, from where he graduated with highest honors in 1820. While at Dartmouth, Marsh taught himself French, Italian, Spanish, and Portuguese.

After leaving school, Marsh tried teaching, but did not enjoy it. He studied law and was admitted to the bar in 1825. He practiced law in Burlington, Vermont, for the next 35 years, at the same time engaging in a variety of business ventures, all of which failed. The illustration on page 27 shows Marsh during this period of his life. He took up politics, and in 1843 he was elected to Congress as a Whig, serving until 1849. Marsh was never a very influential politician, but he proved to have a talent for organization and played a prominent part in the establishment of the Smithsonian Institution.

After his diplomatic service in Turkey and Greece, Marsh returned to Vermont in 1854, and from 1857 to 1859 he was railroad commissioner. During this time he also acquired a reputation as an authority on languages and lectured at Columbia University in New York City and the Lowell Institute in Boston. Fluent in Icelandic, he wrote *A Compendious Grammar of the Old-Northern or Icelandic Language* (1838), *Lectures on the English Language* (1860), and *The Origin and History of the English Language* (1862 and 1885). He spoke a total of 20 languages, including French, German, Italian, Swedish, Norwegian, Danish, and Turkish, as well as some Arabic and Farsi (Persian).

George Perkins Marsh (1801–82) was an American diplomat who spent many years in the countries surrounding the Mediterranean. He warned the American people of the disastrous consequences of excessive deforestation. *(The Granger Collection, New York)*

Marsh also wrote *The Camel, his Organization, Habits, and Uses, with Reference to his Introduction into the United States* (1856). While traveling in Egypt and Arabia, he had become fascinated by the camel and convinced himself that the animal would thrive in the American deserts. He delivered a lecture on the subject at the Smithsonian Institution, which persuaded Congress to import 74 camels. These arrived in Texas in 1856, but the experiment was abandoned due partly to the Civil War and partly to the army's unfamiliarity with camels.

In 1828 Marsh married Harriet Buell, the daughter of a Burlington landowner. They had two sons, but Harriet died in 1833, soon after the birth of George Ozias, and Charles, their first son, died 12 days after his mother. Marsh then married Caroline Crane (1816–1901) in 1839, a teacher, poet, linguist, and feminist. Because of her influence, Marsh supported the feminist cause and took a particular interest in women's education. Marsh died on July 23, 1882, at Vallombrosa, Italy, and is buried in the Protestant cemetery in Rome.

## NATIONAL PARKS AND WILDLIFE RESERVES

In the early years of the 19th century, people began debating the idea of preserving wilderness areas and the wildlife they supported by creating national parks. George Catlin (1796–1872), a self-taught artist who traveled widely through North America, was one of the early champions of this cause. Catlin feared that the westward expansion of settlers would convert vast tracts of land to farms, clear forests, and have a serious effect on the way of life of the Native American peoples. The idea gained acceptance, and in 1864 Congress donated the Yosemite Valley and the Mariposa grove of Sierra redwood trees (*Sequoiadendron giganteum*) to California, to be preserved as a state park.

A state park was not owned or controlled by the federal government, however. Yellowstone was the nation's and the world's first national park. In the years following the end of the American Civil War, General Philip Henry Sheridan (1831–88) embarked on a peacetime campaign to protect Yellowstone, an area where Wyoming, Montana, and Idaho meet. Descriptions of the Yellowstone area had been reaching the eastern United States since the early years of the 19th century, and in 1870 General Sheridan authorized Lieutenant Gustavus Cheyney Doane (1840–92) to provide the military escort to an expedition into Yellowstone that was planned by a group of prominent Montana citizens and led by the surveyor general of the Montana Territory, Henry Dana Washburn (1832–71), accompanied by Nathaniel P. Langford (1832–1911). This led to a second expedition in 1872 led by Langford, who lobbied in Congress to make Yellowstone the world's first national park and suggested that the government could profit by leasing timber rights in the area. On March 1, 1872, President Ulysses S. Grant signed the bill that established the park, in the words of the bill "for the benefit and enjoyment of the people," and Langford was appointed its first superintendent, serving from 1872 to 1877.

Other national parks followed, the next three in 1890, all in California: General Grant, Sequoia, and Yosemite. The Yosemite state park was added to the national park in 1906. Other areas were protected in different ways. In 1891 President Benjamin Harrison established the Yellowstone Timberland Reserve, which was the first forest reserve. In 1903 President Theodore Roosevelt established the first national wildlife refuge at Pelican Island, Florida. National parks, wildlife refuges, and forest reserves were designed to protect wildlife and natural resources. There were also areas containing objects of prehistoric, historic, and scientific importance, and in 1906 the Antiquities Act authorized the president to protect these as national monuments.

By 1916 there were 40 national parks and national monuments, but with no overall strategy for their management. That lack was remedied on August 25, 1916, when President Woodrow Wilson signed into law the National Park Service Organic Act (often called simply the Organic Act), which established the National Park Service (NPS) under the Department of the Interior. More national parks and monuments were designated, all to be managed by the NPS, but the War Department and Forest Service of the Department of Agriculture also controlled areas of importance. In 1933 an executive order transferred 63 of these to the control of the NPS, and in 1970 the General Authorities Act awarded equal status to all the units within the national system. The NPS now administers approximately 380 areas covering more than 130,000 square miles (340,000 $km^2$).

Canada also began establishing national parks toward the end of the 19th century. In November 1885 the government set aside about 10 square miles (25 $km^2$) on the slopes of Sulphur Mountains; that was the first step in creating the Banff National Park, Alberta, in 1887, covering 2,564 square miles (6,640 $km^2$). Others soon followed: Yoho, British Columbia, in 1886; Glacier, British Columbia, in 1886; and Waterton Lakes, Alberta, in 1895. The federal parliament designates Canadian national parks. There are currently 36 national parks and national park reserves—areas set aside to become a national park once land claims are settled. They have a total area of 86,644 square miles (224,466 $km^2$).

North American national parks comprise areas of wilderness in which it is possible to restrict human activities. Visitors are welcome to walk, ride, canoe, and camp, but because the parks exist primarily to preserve the integrity of the landscapes and wildlife there are restrictions on driving vehicles. Britain has a much higher density of population, and so this approach was not feasible. The first 10 national parks in England and Wales were established between 1951 and 1957 under the terms of the National Parks and Access to the Countryside Act, 1949. Three more parks have since been added, bringing the total area to 6,280 square miles (16,265 $km^2$). Each park is managed by its own national park authority, charged with conserving and enhancing the natural beauty of the area, and promoting opportunities for the understanding and enjoyment of the parks' special qualities by the public. Most British national parks consist of open mountain and moorland, but it is not wilderness. The land is privately owned, and some of it is farmed. There are villages and small towns in the national parks, served by roads, but there are restrictions on building and on any kind of industrial development.

Until 2002 there were no national parks in Scotland. In 2000 the Scottish parliament passed the National Parks (Scotland) Act, creating the first two. The Loch Lomond and the Trossachs National Park (720 square miles; 1,865 $km^2$) was formed in 2002, and the Cairngorms National Park (1,466 square miles; 3,800 $km^2$) in 2003. Like the national parks of England and Wales, the Scottish national parks are semi-natural landscapes. As well as conserving and enhancing the natural and cultural heritage of the areas they cover and providing public access for recreation, the parks also aim to promote the sustainable use of the natural resources and economic and social development. The Scottish government also plans to designate one or more marine national parks along the coast.

In addition to the national parks and areas afforded planning protection because of their landscape value, Britain has many nature reserves dedicated to wildlife conservation. These vary greatly in size and are distributed throughout England, Wales, Northern Ireland, and Scotland. Each English and Welsh county has a wildlife trust. These are nonprofit organizations whose members volunteer to manage local reserves. Northern Ireland and Scotland each have one trust covering the entire area. As well as the local reserves, there are reserves specializing in birdlife that are owned and managed by the Royal Society for the Protection of Birds, and national nature reserves managed by government agencies.

Every European and Asian country now has areas set aside as national parks and wildlife reserves. There are national parks in most African countries, and there are also game reserves, some of which are large. The Niassa Game Reserve in northern Mozambique, for instance, covers 16,212 square miles (42,000 $km^2$), and the Selous Game Reserve in Tanzania extends across approximately 19,300 square miles (50,000 $km^2$). The Serengeti National Park in Tanzania occupies about 5,790 square miles (15,000 $km^2$).

The movement that began in the United States, pioneered by conservationists such as John Muir (1838–1914), the Scottish-born naturalist and writer who campaigned for the protection of the Yosemite Valley, spread all over the world. Britain was late in joining, but by the beginning of the 21st century there were national parks and wildlife reserves in almost every country in the world. According to the United Nations Environment Programme, in 1970 the total area of protected lands throughout the world amounted to about 1.07 million square miles (2.78 million $km^2$). By the late 1990s—the most recent figures available—the area had increased to more than 4.63 million square miles (12 million $km^2$).

## HENRY DAVID THOREAU AND WALDEN

Transcendentalism was a philosophy developed by a group of writers in the United States in the 1830s and 1840s, based on the idea that there is no need for organized religion because everything that an individual achieves is part of the divine. Every attempt a person makes to develop and perfect his or her abilities is an expression of the divine. This view was propounded principally by the poet, essayist, and philosopher Ralph Waldo Emerson (1803–82) and Henry David Thoreau (1817–62). Emerson called the transcendentalists "the party of the Future" and summarized his ideas in a 95-page booklet called *Nature,* which he published anonymously in Boston in 1836. Emerson believed that mind was supreme, not matter, and that people are not the victims of their environmental circumstances, but can liberate themselves by developing their consciousness until they find themselves in harmony with nature, which would then satisfy their physical and spiritual needs. Through closeness to nature an individual can transcend the normal and experience the divine. The philosophy inspired the formation of a number of Utopian communities, none of which survived for very long, but it also strongly influenced many American thinkers, and some historians have said that it led to the emphasis on self-help, organization, and drive that characterize American culture.

On July 4, 1845, Thoreau embarked on a transcendentalist experiment in simple living when he moved into a small house he had built for himself on land owned by Emerson. The house was set in *secondary-growth forest*—forest that has grown up naturally on land from which the original, primary forest was cleared—near the shore of Walden Pond. This was not the wilderness; Thoreau's house was 1.5 miles (2.4 km) from his home in Concord, Massachusetts. Thoreau spent one night in jail in July 1846 because of his refusal to pay six years' arrears of poll taxes, owing to his opposition to the war

Henry David Thoreau (1817–62), the American author and naturalist, in about 1855 when he was in his late 30s *(Hulton Archive/Getty Images)*

between Mexico and the United States and his disapproval of slavery. He would have remained in jail longer, but his aunt paid the taxes despite his protests. He left Walden again in August 1846 for a short visit to Mount Katahdin in Maine. Apart from these excursions, Thoreau remained in his house until September 7, 1847.

While he was at Walden, Thoreau wrote an essay, *Civil Disobedience* (also called *Resistance to Civil Government*), inspired by his refusal to pay his taxes, which was published in 1849, and *A Week on the Concord and Merrimack Rivers,* describing a trip he and his elder brother, John, had made in 1839. Thoreau could not find a publisher for this work, and on Emerson's advice he published it himself. Fewer than 300 copies were sold, and it took Thoreau years to pay off the debt he incurred. The incident soured his relations with Emerson. Thoreau also kept a journal of his time at Walden, and he used this as the basis of a book about his experiences and ideas in which he compressed the time he spent at Walden into a single year. The book was called *Walden, or Life in the Woods,* and it was published in 1854. The picture of Thoreau (above left) was made in about 1855, so it shows him as he appeared at about the time of *Walden*'s publication.

The book had little impact during Thoreau's own lifetime. For many years critics dismissed it as amateurish, but in the 1970s, with the rise of the environmental movement with its emphasis on "natural living," it was reappraised. Today it is regarded as a classic account of the virtues of simplicity and living with nature. Thoreau never intended to leave society permanently, and he often walked the short distance to Emerson's house for a meal. He did not mean to set an example for others to follow, and he was not opposed to industry or technology. His aim in simplifying his life was partly to save money and partly to give himself more time to work at his writing. Although not a scientist, he was a keen observer of nature, and the transcendentalist movement to which his work belonged was largely forgotten once the nation became caught up in the Civil War. Thoreau's appeal to modern environmentalists arises from his anti-intellectual transcendentalist belief in intuition as a counterbalance to reason, strongly influenced by English romanticism and Asian religions, and raising the possibility of achieving a better way of life through a close union with, and respect for, the natural world.

David Henry Thoreau (he altered the order of his given names after he left college) was born on July 12, 1817, at Concord, Massachusetts. John Thoreau, his father, was a pencil maker, and Cynthia Dunbar, his mother, was the daughter of Asa Dunbar, who at Harvard in 1766 led America's first student rebellion—over the poor quality of the butter served at meals. Thoreau studied rhetoric, classics, philosophy, mathematics, and science at Harvard University from 1833 to 1837, graduating but later refusing to pay the $5 fee to obtain a master's degree. He taught at Concord College for a time in 1835 during an absence from Harvard, then joined the college faculty in 1837 after graduating. In 1838 he and his brother John opened a grammar school in Concord. The school closed in 1842, when John contracted tetanus and died. Thoreau became friendly with Emerson, who encouraged him to write and introduced him to his own circle of writers, and on April 18, 1841, he moved into Emerson's house and worked for him as editorial assistant, gardener, repair man, and tutor to Emerson's children. In 1844 he left Emerson and went to work in the family pencil factory, where he spent most of his working life. In 1845 he began his experiment in living at Walden.

When he left Walden, Thoreau became increasingly interested in natural history, especially in botany, and he was a great admirer of Charles Darwin (*see* "Darwin and the *Beagle*" on pages 86–90). He kept careful notes and wrote an essay, "The Succession of Forest Trees," describing the natural regeneration of woodland that had been burned or cleared.

Thoreau first showed symptoms of tuberculosis in 1835. One night in 1859 he went out during a rainstorm to count *tree rings*—alternately pale and dark rings, visible in a cross section through a tree trunk, that mark the annual spring (pale ring) and late summer and fall (dark ring) growth of the tree. He caught bronchitis, and from that time his health began to deteriorate until eventually he was bedridden. He died at Concord on May 6, 1862. Emerson wrote his eulogy.

## ALDO LEOPOLD AND PRESERVING WILDERNESS

The Gila National Forest covers approximately 5,156 square miles (13,355 $km^2$) in New Mexico. It was established in 1905 and is the sixth largest national forest in the continental United States. Gila Forest also contains the Gila Wilderness. Designated by the Forest Service on June 3, 1924, this was the nation's first forest wilderness area. It covers about 870 square miles (2,258 $km^2$), and Aldo Leopold (1887–1948) was instrumental in persuading the government to preserve the area. Leopold was trained as a forester and forest manager. He was also a game manager and a pioneer of *wildlife management,* which is the management of an area in such a way as to maintain certain of its animal populations at a desirable level determined by the managers. Leopold was also an ecologist, environmentalist, and author, whose most famous book, *A Sand County Almanac,* a series of 41 essays published posthumously in 1949, inspired environmentalists through its vision and the quality of Leopold's writing. The following two brief passages give a flavor of the work:

> [Passage one] It is a century now since Darwin gave us the first glimpse of the origin of the species. We know now what was unknown to all the preceding caravan of generations: that men are only fellow-voyagers with other creatures in the odyssey of evolution. This new knowledge should have given us, by this time, a sense of kinship with fellow-creatures; a wish to live and let live; a sense of wonder over the magnitude and duration of the biotic enterprise.

and again:

> [Passage two] Acts of creation are ordinarily reserved for gods and poets, but humbler folk may circumvent this restriction if they know how. To plant a pine, for example, one need be neither god nor poet; one need only own a good shovel. By virtue of this curious loophole in the rules, any clodhopper may say: Let there be a tree—and there will be one.
>
> If his back be strong and his shovel sharp, there may eventually be ten thousand. And in the seventh year he may lean upon his shovel, and look upon his trees, and find them good.

Aldo Leopold was born in Burlington, Iowa, on January 11, 1887, and he grew up with a love of the outdoors. The Leopold family took their summer vacations in Les Cheneaux Islands, Michigan, a group of 36 small islands, some of them inhabited, along 12 miles (19 km) of the shore of Lake Huron. Leopold attended Lawrenceville School, in Lawrenceville, New Jersey, but his enthusiasm for being outdoors meant he achieved poor grades. From Lawrenceville he went to the Yale University School of Forestry, where in 1909 he graduated with a master's degree in forestry. He joined the Forest Service the same year and worked as a ranger and later a supervisor in Arizona and New Mexico. In 1924 he was transferred to the Forest Products Laboratory in Madison, Wisconsin, as its associate director. He was not happy working in the laboratory, and in 1928 Leopold left the Forest Service and became an independent contractor, mainly specializing in wildlife and game surveys.

Leopold had acquired considerable experience in game management, and in 1933 he was appointed professor of game management, in the Agricultural Economics Department of the University of Wisconsin–Madison. He continued teaching at the university for the rest of his life.

In 1935 Leopold became a founding member of the Wilderness Society. That was also the year in which he bought a rundown farm by the Wisconsin River, north of Madison. The only building still standing was a former chicken coop, and Leopold, his wife, Estella, and their five children converted it into a small cabin where the family slept. They called it The Shack and spent weekends there planting trees—eventually thousands of them. During that time, spent planting to restore the depleted land and hiking through the surrounding countryside, Leopold developed what he came to call a land ethic. The land ethic, he wrote in *A Sand County Almanac,* "simply enlarges the boundaries of the community to include soils, waters, plants and animals, or collectively: the land." The ethic imposed a duty of care, to preserve and enhance the capacity of the land for self-renewal. He enlarged on this a little in the following excerpt:

> It is inconceivable to me that an ethical relation to land can exist without love, respect, and admiration for land, and a high regard for

its value. By value, I of course mean something broader than mere economic value; I mean value in the philosophical sense.

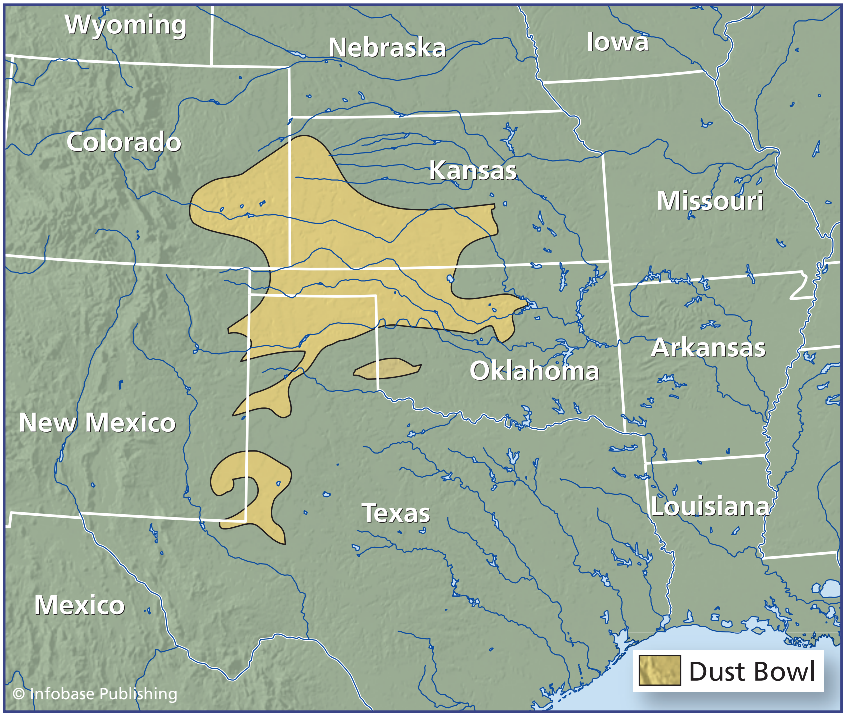
By land, Leopold meant all living organisms, and he demonstrated the need for a land ethic by showing that when a population was threatened with extinction, conservationists were reduced to inventing some spurious economic argument to justify saving it. "Of the 22,000 higher plants and animals native to Wisconsin," he wrote, "it is doubtful whether more than 5 percent can be sold, fed, eaten, or otherwise put to economic use. Yet these creatures are members of the biotic community and if (as I believe) its stability depends on its integrity they are entitled to continuance."

In addition to *A Sand County Almanac,* Leopold wrote textbooks, as well as many reviews, technical reports, and poems. He was an adviser on conservation to the United Nations. Aldo Leopold died from a heart attack on April 21, 1948, while helping his neighbors fight a grass fire close to The Shack.

## THE MEANING OF THE DUST BOWL

At intervals of 20 to 23 years, the Great Plains of the United States experience drought, sometimes severe and at other times less so. No one knows the reason for this climatic cycle except that it is entirely natural. It may be linked to changes in energy output from the Sun. There was drought in the 1950s, an especially severe drought in the 1970s, and drought returned again in the 1990s.

The worst drought of modern times occurred in the 1930s. Its cause was natural, just like other American droughts, but this time its effects were exacerbated by the way the land was being used. At its peak the drought affected more than three-quarters of the United States. The map shows the area that suffered worst. This is the area that came to be called the dust bowl. In 1934 the *Yearbook of Agriculture* published by the U.S. Department of Agriculture reported that: "Approximately 35 million acres of formerly cultivated land have essentially been destroyed for crop production. . . . 100 million acres now in crops have lost all or most of the topsoil; 125 million acres of land now in crops are rapidly losing topsoil." It is difficult to picture an area of 100 million acres, but it is 156,250 square miles (404,688 km$^2$), an area almost the size of California.




The drought of the 1930s affected more than three-quarters of the United States. The shaded area in this map shows the area where the drought was most severe.

Originally prairie grasslands covered the Great Plains. Grasses were the most abundant plants, some growing as tussocks three feet (90 cm) tall. Many prairie grasses have deep roots, and the plants bind the soil and prevent erosion. The part of the plant that is above ground slows the wind at ground level, reducing its power to blow away soil particles, and grass roots form a mat that traps soil particles among its fibers. Prairie grasses are quite different from the grasses used to make lawns and sport fields. They are adapted to growing in a climate that is generally dry and drought-prone. Boise City, Idaho, for instance, has an average annual rainfall of 16.5 inches (419 mm) and Dodge City, Kansas, 20.4 inches (518 mm). Central Park in New York City, in contrast, receives an average 44.4 inches (1,129 mm) of rain a year (snowfall is routinely converted to the equivalent rainfall and added to the rainfall figure).

During the 19th century, a stream of settlers moved westward across the United States, seeking a new and better life. Most were country folk who needed land they could farm. The government encouraged this migration. After more than 70 years of controversy over the use of public lands, the Homestead Act of 1862 came into force on January 1, 1863. The act offered 160 acres (65 hectares) of land to anyone. If, after five years, the homesteader had built a house on it, dug a well, plowed 10 acres (4 ha), fenced part of the land, and lived on it the whole of that time, the land became the property of the homesteader. The offer was made to newly arrived immigrants as well as to existing U.S. citizens. Railroad companies and financial speculators acquired much of the land, but by 1900 about 600,000 farmers had settled on about 80 million acres (32.4 million ha). These homesteaders joined the many other farming families who had moved onto the plains earlier.

To the settlers the prairie grasslands looked much like the grasslands they had known in the East, or like the European grasslands the new immigrants remembered. No one thought to tell them that the eastern and European grasslands grow in a much wetter climate. So the settlers set about farming the way they knew. They repeatedly burned the grasses then plowed the land and sowed wheat and other crops. The soil was fertile and harvests were good in rainy years. When there was drought, which happened from time to time, the crops failed and some farmers were ruined. They were forced to abandon their farms and homes, but after a year or two the rains returned, new homes were built, and farming resumed under new owners.

The settlers used horses as draft animals, and plowing and harrowing were slow, hard work until, in about 1915, tractors began to appear. These made the work much easier, and farms expanded. In 1910 there were less than 5 million acres (2 million ha) of land growing wheat in Kansas. By 1919 the area had increased to more than 12 million acres (5 million ha). The increase was achieved by plowing more of the prairie. Then combine harvesters were invented, which speeded the harvesting operation. All this machinery was expensive, but by 1919 wheat prices were rising fast enough to pay for it and farmers were prospering. The land itself was also becoming easier to till. After decades of cultivation, the tough clods of prairie soil the first homesteaders had struggled to break up had disappeared, and the soil had been worked into a fine, friable texture that was ideal for sowing cereals.

In 1929 the stock market crashed, triggering a huge and rapid contraction of the national economy, leading to the depression of the 1930s. During the depression, prices fell and falling wheat prices forced farmers to work the land more intensively in order to increase grain production and maintain their living standards. Despite their efforts, farming incomes gradually fell, and the plight of the poorest farmers became desperate. They were still able to farm, however, because the weather remained favorable. Between 1927 and 1933, the annual rainfall in Nebraska, Iowa, and Kansas was 5 inches (127 mm) above average.

Unnoticed by the farmers, change was coming. The global climate was becoming warmer, and one consequence of this climatic change was an increase in the number of days when winds in middle latitudes were from a westerly direction. Rainfall increased in lands on the eastern sides of the oceans because they were more frequently exposed to winds that had crossed the sea. On the prairies, on the other hand, the westerly winds lost their moisture as they crossed the Rockies, and the rainfall decreased to well below what had been the average. Crops began to fail, and the remaining prairie grasses died back. Then there was no vegetation to protect the light, friable, well-tilled soil from the incessant winds.

Prairie grasses always died during severe drought, but their roots bound the soil into lumps that dried into hard clods. When the rains returned, the roots recovered. That is how the grasses survived, and in doing so they prevented the soil from eroding. The farmers had broken up those tough clods, and the soil was now light, almost a powder, and it began to blow. There were 14 severe dust storms in 1932, and in 1933 there were 38. They called them black blizzards, and the photograph on page 40 shows why. The dust, consisting of topsoil together with the seeds the farmers had sowed and any fertilizer they had applied, approached like a wall. When it arrived, it blocked out the sunlight. Dust from the ruined prairie farms settled on ships 300 miles (483 km) from the coast. Ducks and geese fell dead from the sky, choked by the dust they had flown through. At one point a single dust cloud, 3 miles (4.8 km) high, extended all the way from Canada to Texas and from Montana to Ohio, an area of 1.35 million square miles (3.5 million $km^2$). The drought continued until 1940–41, when the rains returned and the prairie grasses recovered.

Families from the dust bowl abandoned the wreckage of their farms. Altogether 2.5 million people migrated, 200,000 of them westward to California. Already impoverished by the collapse in prices, it was the depression that had ruined them rather than the drought, but nevertheless the drought was a lesson the nation took to heart. The lesson was that prairie soils are fragile and must be farmed with care, and that the native grasses are adapted to the climate. Prairie grasses can survive severe drought while protecting the soil at the same time. In 1935, as a direct response to the drought, the Soil Conservation

A wall of dust approaching a Kansas town on October 4, 1935, during the years of drought that produced the dust bowl *(Historic NWS Collection)*

Service was formed within the Department of Agriculture (USDA). The service still exists as a branch of the USDA, but its name has been changed to the Natural Resources Conservation Service.

## PUBLIC OR PRIVATE? "THE TRAGEDY OF THE COMMONS"

William Forster Lloyd (1795–1852) was a distinguished English economist. He was a fellow of the Royal Society, and in the 1830s he was Drummond Professor of Political Economy at the University of Oxford. Lloyd was especially interested in the extent to which the satisfaction a consumer derives from a good or service decreases with each incremental increase in its supply—an effect known as diminishing marginal utility. He was also concerned about population, and in 1833 he published *Two Lectures on the Checks to Population.* As his title suggests, the book was based on the texts of two of his lectures.

In his book Lloyd recounted a parable, which he called "The Tragedy of the Commons." This suggested that when a resource is freely available to all—he called it a commons—overuse will inevitably destroy it. The idea was not new. Several ancient Greek writers made the same point, and it is enshrined in popular belief, expressed by sayings such as: "You don't appreciate what you get for free." In 1968 Garrett Hardin (1915–2003), professor of human ecology at the University of California, Santa Barbara, revived Lloyd's work in an essay with the same title in the magazine *Science.* Hardin based his essay on Lloyd's (inaccurately referring to Lloyd as an amateur mathematician), but he extended it and expressed it in more modern language.

Both Lloyd and Hardin illustrated "The Tragedy of the Commons" by the example of an area of pasture on which all the cattle-owners in the area are permitted to graze their animals free of charge. Each cattle-owner seeks to maximize his gain and in doing so considers the relative advantage and disadvantage—the positive and negative utility—of adding one more animal to the herd. The positive utility is that the cattle-owner receives the whole of the profit from the sale of the additional animal. Call that +1. The negative utility is that the extra grazing contributes to the deterioration of the pasture. Call that -1. However, the negative utility is shared among all the cattle-owners using the pasture, so the individual owner suffers a negative utility that is only a fraction of -1. Consequently, the positive utility is bound to exceed the negative utility. But since this is true for each of the cattle-owners and the arithmetic remains the same for each additional animal, it is inevitable that more and more animals will be brought onto the pasture until overgrazing totally destroys the vegetation, rendering the pasture useless to all the owners.

Hardin was arguing against what he saw as the dangers of overpopulation, a problem to which there can be no technical solution in the sense that increasing the availability of resources must eventually reach a limit. In the example, the problem of the cattle-owners and overgrazing also has no technical solution; it might be possible to fertilize and reseed the pasture to make it more productive, or expand its area, but this would merely postpone its destruction; it cannot prevent it. Hardin said that problems of this kind can be solved, but only by a change in attitudes and behavior. He asserted: "The only way we can preserve and nurture other and more precious freedoms is by relinquishing the freedom to breed, and that very soon." Some economists, however, have used the essay as an argument for transferring publicly owned resources, or commons, to private ownership.

Probably few people knew of Lloyd's essay until Hardin drew attention to it, but when he did it stimulated a vigorous debate about the best way to manage resources, and the *Science* article became required reading for environmentalists. The issue was controversial because commons in the sense of common land really exist and have done for centuries, and they are sustainable indefinitely. They do not become overexploited because there are strict rules governing their use, and it would be against the law for anyone who is not a commoner to attempt to gain access to them.

The concept of a commons originated in Great Britain and was also introduced in several other countries, including the United States. Customs vary from country to country, but in Great Britain all land is owned, so it is a mistake to suppose that the commons are the common property of all. They are not. A common is an area over which certain individuals apart from the owner, called commoners, have specified rights. In England and Wales (the tradition is different in Scotland), these rights include pasture (the right to graze livestock), piscary (the right to catch fish), turbary (the right to remove turfs for use as fuel), mast (also called pannage; the right to turn pigs onto the land in autumn to feed on acorns and other nuts); estovers (the right to collect small trees and fallen wood for fuel); and common in the soil (the right to remove sand or gravel). In the Middle Ages, on some commons a commoner was permitted to erect a house provided he started work at dawn and by sunset had a roof over his head, a fire in his hearth, and had declared the place his dwelling. That rule was repealed by an act of Parliament, which is probably as well; nowadays a developer could establish a trailer park in that time. Management of the commons is the responsibility of the commoners themselves, who meet at regular intervals to decide how much exploitation of the various resources they should permit.

These rights are very ancient, often predating written laws. In recent decades, the commons have deteriorated in some places, but through neglect rather than overexploitation. Commoners, especially in lowland areas, found better-paid jobs and ceased to exercise their traditional rights and as the use of the commons—especially of pasture—decreased, the land reverted to scrub and eventually became woodland.

Conservation of resources is a major aspect of overall care for the natural environment. Many resources are finite, and even those which are not, such as the air, can easily be polluted. Garrett Hardin undoubtedly performed a valuable service in drawing attention to Lloyd's original parable and updating it, but it was misleading to describe as a commons a resource that has no owner and to which many have free access. That is not to say that the problem Lloyd and Hardin addressed cannot occur. The widespread depletion of commercial fish stocks due to overfishing is a clear example.

# 3

# The Chain of Being

Ecology is the study of communities and the relationships among their members and between those members and their chemical and physical surroundings. A modern science, it began in the 19th century and developed during the 20th, but its origins lie in the more distant past, with the early students of natural history. Like all scientists, the natural historians discussed their observations and exchanged letters, but in doing so they faced a difficulty. They needed to discuss plants and animals, yet to do that they needed to be able to give them unambiguous names. This is not difficult when the plant or animal is familiar and distinctive. The various types of European oak trees would be familiar to European naturalists, as would the European mammals, reptiles, and most birds, but problems arose when an observer wished to distinguish among closely related organisms that were almost identical in appearance.

As they moved toward solving the problem of naming organisms, scientists also found themselves commenting on the behavior of animals and the environmental requirements of plants. This brought them close to what would now be called an ecological approach to their subjects. The observation that a particular plant or animal usually occurs in places with a certain type of soil and climate sets the organism in an environmental context; when the observation really is an observation, based on examining the organism in the real world rather than relying on tradition or hearsay, it is ecological in character. Scientists found that their new observations tended to confirm one of the most ancient of ideas, that of a Great Chain of Being, with minerals and metals at the base and human beings at the pinnacle.

This chapter traces some of these beginnings, starting with John Ray (1627–1705), the man often described as the founder of natural history observation. Ray tried to impose order on the names people were using to identify plants and animals. The chapter continues by explaining how the concept of a great chain of being developed and how scientists interpreted the ways in which organisms adapt to their environments, then tells how the interdependence of organisms came to be recognized. It ends with the work of Carl Linnaeus (1707–78), who popularized the system for naming species that is still in use today. Finally, the chapter introduces a more modern puzzle: What is a species?

## JOHN RAY AND THE CLASSIFICATION OF PLANTS

Daffodils are commonplace. They grow everywhere, and when daffodils are mentioned in a book, most people probably know what plant the author has in mind. But daffodils have alternative names, and the author could have written about daffy-down-dillies, lent lilies, porillons, or narcissus. These are all names for the same plant, but does everyone know that? Surely everyone is familiar with holly, but how many would recognize it if the author, quite legitimately, called it hulver bush, holm, or holy tree? Dandelions, whose name is a corruption of the French *dents de lion* (lion's teeth), are also called priest's crowns and swine's snouts. These are all names in the English language. When the list extends to other languages, it grows rapidly longer. Most familiar plants and animals have several common names, and even in the same language sometimes these can cause confusion. The large deer known in North America as a moose is called an elk in Europe, while the North American elk is known in Europe as the red deer. The North American caribou is the same animal as the European reindeer.

The difficulty over names that naturalists faced may seem artificial. After all, daffodil, dandelion, and holly are generally accepted as the common names of these plants, and the animal examples are limited in number. This is true today, but local names for plants and animals were much more widely used centuries ago, when travel was slower and more difficult. Naturalists needed a more reliable naming system, but for a time they had to resort to lengthy descriptions of the specimens they were discussing. Even then there were problems because specimens of the same organism collected in different places often vary in size and color.

Between 1686 and 1704, the English naturalist John Ray published *Historia plantarum* (History of plants), a huge, three-volume work that was a greatly expanded version of his *Methodus plantarum nova* (New system of plants), published in 1682, and revised in 1703 as *Methodus plantarum emendata.* Ray was the first naturalist to distinguish, in his *Methodus,* between plants with one *cotyledon*—seed leaf—or two, placing them in two divisions he called Monocotyledones and Dicotyledones, although this distinction had been noted earlier by the English plant anatomist Nehemiah Grew (1641–1712). The distinction is still used, although the monocots and dicots, as they are now known, are no longer placed in separate divisions. He also distinguished between flowering and nonflowering plants. Ray devised a classification system for plants and described it in the *Methodus.* In the first edition, he based his system on fruits, but in the amended edition he based it on flowers—he was the first person to use the terms *petal* and *pollen.* The *Historia plantarum* applied his classification to every plant he knew or about which he had read. Together, the three volumes described 18,625 plant species, and Ray was the first person to attempt a definition of the term *species.*

John Ray also wrote about animals. Georges Cuvier (1769–1832), the French naturalist and zoologist, described Ray's work as "the basis of all modern zoology." Ray worked out a classification for tetrapods and snakes (*Synopsis methodica quadrupedum et serpenti generis;* Systematic summary of the kinds of quadrupeds and snakes), published in 1693, and for fishes and birds (*Synopsis methodica avium et piscium;* Systematic summary of birds and fishes), published in 1713. He also commenced a classification of insects, based on *metamorphosis*—the radical transformation from the larval to adult form—but died before completing it.

John Ray (until 1670 he spelled his name Wray) was born on November 29, 1627, in Black Notley, a village near Braintree, Essex, to the east of London, where his father was a blacksmith. He commenced his education at the school in Braintree. When he was 16, he entered Catherine Hall (now St. Catherine's College) at the University of Cambridge, but after about 20 months he transferred to Trinity

College, where he graduated in 1647 or 1648. He became a fellow of Trinity in 1649, obtained his master's degree in 1651, and went on to hold several college positions. He was appointed a lecturer in Greek in 1651, mathematics in 1653, and humanity in 1655. As was the custom, he also preached in the college chapel prior to his ordination in 1660. Ray had to give up his fellowship in 1662 because of his refusal to subscribe to the 1661 Act of Uniformity, a law that required all Church of England clergy to use the Book of Common Prayer and stipulated that only bishops could ordain ministers. Thereafter he was forbidden to teach in any university and could not hold any church appointment. His career prospects must have seemed bleak.

One of Ray's Cambridge students was Francis Willughby (1635–72), a wealthy aristocrat who later became a skilled ornithologist and ichthyologist. Ray and Willughby became close friends, and Ray depended on the financial support he received from Willughby. Ray toured Europe with Willughby and two other pupils from 1663 to 1666, returning laden with specimens, on which the two friends planned to base classifications of animals and plants. Willughby undertook to classify the animals, but died in 1672, leaving a vast but incomplete manuscript for Ray to edit. In 1667 Ray and Willughby submitted a paper "Experiments concerning the motion of sap in trees" to the Royal Society; it was published in the *Philosophical Transactions of the Royal Society,* and in 1669 Ray was elected a fellow of the Royal Society.

Ray's first botanical book was *Catalogus plantarum circa Cantabrigium* (Catalog of plants around Cambridge), published in 1660. This was the first flora (list of plants) of Cambridgeshire, and Ray followed it with *Catalogus plantarum Angliae* (Catalog of English plants) in 1670 with a second edition in 1677, in which the plants were listed alphabetically. In 1690, with a second edition in 1696, Ray published *Synopsis methodica stirpium Britannicarum* (Methodical summary of notable British plants), in which the entries were arranged according to his classification. These were the first British floras.

After his death, Willughby had left Ray an annuity of six shillings a year for life and charged him with educating his two sons, Francis and Thomas. John Ray married Margaret Oakley in 1673, and the couple went to live in Sutton Coldfield, near Birmingham. She was 19 years old and a member of the Willughby household. In 1677 they moved to Faulkbourne Hall in Essex. After his father died in 1656, Ray had built a house he called Dewlands in Black Notley for his widowed mother, and following her death in 1679 John and Margaret moved into it. They had four daughters. Ray's health had started to deteriorate years earlier, and he remained in poor health. He lived quietly in Black Notley, corresponding with friends and colleagues and writing books. He died on January 17, 1705, and at his own request he was buried in the village churchyard; he was too humble to feel worthy of being buried inside the church.

## ADAPTATION AND THE GREAT CHAIN OF BEING

John Ray believed there was a good reason why birds reproduce by laying eggs. He pointed out that if their young developed in an internal womb, like those of mammals, pregnant birds would be too heavy to fly and would therefore be very vulnerable to predators. Consequently, pregnant birds would be killed, and before long all birds would disappear. If birds bore live young, there could be no birds. Reproduction by egg-laying was one example of the way birds were fitted to life in their aerial environment, and close examination revealed that every type of plant and animal was equipped for its way of life. To express the idea in more modern language, organisms are adapted to their environments. Like other naturalists of the time, Ray saw adaptation as a manifestation of the way God had ordered the world, fitting every organism for its assigned role in nature.

The recognition that each organism was equipped for its own way of life gave support to a much older idea, of a Great Chain of Being. At least since the days of ancient Greece, people had accepted that all living things could be compared with human beings, and it was but a short step from there to using human beings as the standard against which all other living things should be measured. John Ray also accepted this idea, as did all of his fellow naturalists.

Medieval scientists did not distinguish between living and nonliving objects, believing that since plants and animals were made from material parts, like complex machines, there was a continuity extending from minerals to plants to animals. Consequently, they placed minerals at the base of the Great Chain of Being and God at the top. The basic chain was, therefore, starting at the bottom: minerals, plants, animals, humans, angels, God.

Some of these broad categories were subdivided. The hierarchy of humans, for instance, went, again starting from the bottom: gypsies, thieves and pirates, actors, beggars, shepherds and herders, tenant farmers, domestic servants, soldiers and town watchmen, yeomen farmers, tradespersons, messengers, pages, squires, ladies-in-waiting, knights and local officials, barons and baronesses, viscounts and viscountesses, earls and countesses, marquises and marchionesses, dukes and duchesses, kings and queens. Monks and clergy had a parallel hierarchy of their own. Similarly, each group of nonhumans also had a hierarchy, with one organism, known as a primate, at the top. Among mammals the primate was sometimes the lion and sometimes the elephant; among birds it was the eagle; and among fishes it was the whale or dolphin (which were then classed as fishes). The oak tree was the primate among plants, and the hierarchy, working downward, went: trees, shrubs, cereal crops, herbs, ferns, weeds, fungus, and moss. There were also nonliving hierarchies. Diamond was the primate among precious stones, gold among metals, and marble among rocks.

This view of the world had two important implications. The first, relating to humans, was that since God had ordained the chain, every individual has a rank in society and must know and keep to his or her place. Not only was social mobility inconceivable, any attempt to rise socially amounted to rebellion against the state and, much worse, against God. In addition to this political conservatism, there was also a moral imperative to behave in ways appropriate to a rational, spiritual being and not to display the lower, bestial instincts such as gluttony (eating like a pig), spitefulness (like a shrew), and lechery (like a goat). Of course, one could also emulate one of the primates by being as brave as a lion, wise as an elephant, or strong as an oak tree. When people describe someone as being "a rough diamond" or having a "heart of gold," they take their images from the Great Chain of Being.

The second implication concerned nonhumans and was equally conservative. Since God had created every possible being, there could be no gaps in the chain, and each organism could have but two neighbors, one a rank above and the other a rank below. If naturalists discovered what appeared to be a gap between two ranks, it meant only that they had not identified the linking organism. Flying fishes were held to form a link between fishes and birds, and such marine invertebrates as coral polyps and sea anemones linked plants and animals—and were known as zoophytes, a word meaning animal-plants. As the naturalists of the 17th and 18th centuries discovered more and more previously unknown plants and animals, each of them had to be fitted into the increasingly elaborate hierarchy. It was impossible for an organism to become extinct or, of course, for a new one to appear. John Ray knew that fossils were the remains or traces of plants and animals unlike any existing at the present time, but he could not bring himself to believe that organisms had ceased to exist. The pattern was absolutely static.

There was a way to deal with the problem of fossils, however, and it was Charles Bonnet (1720–93), a naturalist in Geneva (which

## CHARLES BONNET (1720–1793), AND THE DISCOVERY OF PARTHENOGENESIS

Charles Bonnet was born on March 13, 1720, in Geneva, into a wealthy French family that had been driven out of France in the 16th century by religious persecution. Geneva was then an independent city-state (it became part of Switzerland in 1815) and his father, Pierre Bonnet, was a member of the Geneva Grand Council (Grosser Rat); his mother was Anne-Marie Lullin de Châteauvieux. Charles Bonnet became partially deaf when he was seven, and because other children teased him his parents hired tutors to commence his education. When he grew up, he was a lawyer by profession, but he never enjoyed the law, much preferring the study of natural history, in which he was a student of the French naturalist René-Antoine Ferchault de Réaumur (1683–1757). Bonnet finally broke his connection with the law in 1743. In that year he received his doctorate in law and was also elected a fellow of the Royal Society.

Bonnet earned his fellowship of the Royal Society by his studies of regeneration in invertebrate animals and his demonstration that caterpillars and adult butterflies breathe through pores, now called *stomata,* in their *exoskeletons*—the horny outer covering that encloses the bodies of all crustaceans, spiders, mites, insects, centipedes, and millipedes. In 1740 he submitted to the French Academy of Sciences a paper describing a series of experiments by which he had established that aphids can reproduce parthenogenetically, for which he was made a corresponding member of the academy. In 1741 he commenced the studies of regeneration and reproduction by budding in freshwater hydra that won him his fellowship of the Royal Society. In 1745 he published *Traité d'insectologie* (Treatise on entomology). This was a work on experimental entomology, published in two parts, in which Bonnet described his work on reproduction in aphids and also developed was then a city-state and not part of Switzerland) who discovered it (see the sidebar starting on page 50). In 1770 Bonnet proposed in *La palingénésie philosophique* (Philosophical regeneration) that from time to time the Earth is struck by natural disasters. Every time this happens most organisms are killed, but the survivors advance by one rank in the hierarchy. After the next disaster, humans will become angels and trees will become simple animals. His view hinted at an evolutionary process, and Bonnet is said to have been the first scientist to use the word *evolution* in this sense.

Bonnet's concept of evolution—if that is what it was—was not the modern concept, however. He believed that types of organisms were absolutely separate and supported this by his theory of reproduction.

his theory of a Great Chain of Being. Then he turned to botany, specializing in the study of plant leaves. In 1754 he published *Recherches sur l'usage des feuilles dans les plantes, et sur quelques autres sujets relatif à l'histoire de la végétation* (Researches on the ways plants use their leaves, and on several other subjects relating to the natural history of vegetation), in which he suggested that plants are able to sense their surroundings and respond to them.

By the 1750s his eyesight was deteriorating, and it became impossible for him to use a microscope or to study small objects, so he turned to philosophy. He wrote several more books in his later years, including, in 1770, *La palingénésie philosophique, ou idées sur l'état passé et sur l'état future des êtres vivants: ouvrage destiné à servir de supplement aux derniers écrits de l'auteur et qui contient principalement le précis de ses recherches sur le christianisme* (Philosophical regeneration, or ideas on the past and future states of living beings: a work intended to serve as a supplement to the author's later writings and that contains principally a summary of his researches into Christianity). An English language translation was published in 1787 with the title *Philosophical and Critical Inquiries Concerning Christianity.* In this work Bonnet proposes that the female body contains all future generations in miniature form, one inside another like Russian dolls. His complete works were published between 1779 and 1783 by Samuel Fauche of Neuchâtel, Switzerland, in 18 volumes with the general title *Oeuvres d'histoire naturelle et de philosophie* (Works on natural history and philosophy).

Bonnet led a quiet life, never leaving Switzerland. He was a member of the Grand Council of Geneva from 1752 to 1768, but apart from that he took no part in public affairs. In 1755 he married Marie-Jeanne de la Rive. They had no children. After leaving the council in 1768, he retired to his estate at Genthod, beside Lake Geneva, where he died after a long illness on May 20, 1793.

This held that from birth every female of all species contains within her body an infinite series of fully formed individuals, one inside another like Russian matrushka dolls. Eventually, however, Bonnet had to accept that the chain of being was only one possible explanation for the abundance of organisms naturalists were studying, and there could be other explanations. The chain must have branches, he thought, and admitted that this would mean there were gaps between the branches, and it seemed evident that some organisms had appeared on Earth later than others. He preferred the chain, however, because it conformed to the static arrangement of organisms in which be believed—created by God and preserved by a reproductive system based on an endless succession of preformed individuals.

As naturalists traveled the world, gathering specimens of previously unknown organisms, the Great Chain of Being became increasingly implausible. There were simply too many plants and animals for them to be arranged in the simple linear order the chain demanded. An entirely new way for classifying organisms was needed, one that allowed for many branches, and as naturalists came to recognize this need they were also coming to appreciate the extent to which organisms are interdependent, so their relationships form not a straight-line chain, but a highly intricate network.

## WILLIAM DERHAM AND THE INTERDEPENDENCE OF ORGANISMS

In the 17th century many English scientists sought to demonstrate that their studies of the natural world revealed the wisdom and benevolence of God. Sir Isaac Newton (1642–1727) was one of the founders of this movement, together with his contemporary, the physicist Robert Boyle (1627–91), who was deeply interested in theology and learned Hebrew, Greek, and Syriac in order to read religious texts in their original languages. Boyle was also wealthy, and in his will he bequeathed funds for a series of annual lectures aimed at defending the Christian religion against all others. The tradition continues, and a Boyle lecture is still delivered each year. In 1711 and 1712 the Boyle lecturer was William Derham (1657–1735), an Anglican clergyman and natural historian. Derham published his Boyle lectures in 1713 as a book entitled *Physico-Theology; or a Demonstration of the Being and Attributes of GOD, from His Works of Creation.*

In 1691 John Ray had published his book *Wisdom of God Manifested in the Works of the Creation,* and Derham published a new edition of this work, also in 1713. Derham developed Ray's ideas, especially the argument from design that Ray had introduced. This argument aims to use the complexity of living organisms to prove the necessity for a designer with divine powers: God must exist because how else can the intricacies of nature have been designed?

Derham and those who shared his view of the natural world fully accepted, indeed rejoiced in, the complexity of the networks of relationships that they found linking organisms. They considered this evidence of God's work and marveled at the way every organism performed a function that contributed to the smooth running of the whole of creation. Some organisms provided food for others, some removed wastes, while others prevented particular animals proliferating to become pests. Derham asked himself why, with so many kinds of animals each with a great capacity for reproduction, the world does not become overpopulated. He thought the answer was that God gave each creature a reproductive capacity matched to its longevity. Long-lived animals have few offspring, so they do not overstock the world, and animals that reproduce rapidly are very useful as food to humans or other animals. Everything had its place, even the organisms that harm humans. These, the naturalists argued, served God's purpose of punishing sinners and teaching people wisdom. This overall philosophy came to be called natural theology. Natural theologians believed humans were entitled to exploit other species because that was what God had intended.

Organisms did not overpopulate their surroundings, despite their capacity to do so. Natural theologians saw in this God's plan to maintain a harmonious balance in the world, a balance of nature. This is an idea that still emerges whenever people protest against technologies that they believe would disturb the natural harmony, but it is deeply flawed, because, like the Great Chain of Being, it is totally static, allowing no possibility of change and, therefore, no appropriate response to unavoidable changes in the physical world. It also means that no human interference in the natural world could ever be harmful, because the balance would restore itself automatically.

Derham clearly recognized, however, the extent to which organisms were interdependent. He was not the only person to do so. Richard Bradley (1688–1732), an English writer on horticulture, had observed that many insects feed on only one type of plant, and he advised growers not to kill birds that feed on those insects because they help control pests. Natural theologians might disagree, but writers familiar with rural life, such as Bradley and Gilbert White (*see* "Controlling Rests to Improve Crop Yields" on pages 7–11), knew that some animals could become crop pests, and farmers and growers were permitted to reduce their populations. Living organisms inhabited networks of interdependency within which life for all of them was a struggle to survive and reproduce. This picture of the world that began to emerge in the latter part of the 17th century led to the ecological theories of the 19th and 20th centuries.

William Derham was born on November 26, 1657, at Stoulton, Worcestershire, in the English West Midlands. He was educated at Blockley Grammar School in Blockley, Gloucestershire, and in 1675 he entered Trinity College, University of Oxford. He graduated in 1679 and was ordained into the Church of England in 1681. He gained a master's degree in 1683, and in 1730 he received a doctorate in divinity. He was a clergyman for the whole of his adult life. Following his ordination in 1681, he was appointed vicar of Wargrave, Berkshire, where he remained until 1689, when he became vicar of Upminster, Essex. He remained in Upminster until his death on April 5, 1735.

Derham was elected a fellow of the Royal Society in 1702. In addition to his work on natural history, he wrote about clocks—his first book was *The Artificial Clockmaker,* published in 1696—as well as astronomy and meteorology. He edited works by John Ray, and in 1713 he published Ray's *Synopsis methodica piscium* (Systematic summary of birds and fishes), and new editions of his *Physico-Theological Discourses* and *The Wisdom of God Manifested in the Works of the Creation.* In 1705 he edited the posthumous works of Robert Hooke (1635–1703) and in 1726 Hooke's *Philosophical Experiments.*

## LINNAEUS AND BINOMIAL NOMENCLATURE

At the same time as natural theologians such as William Derham were seeking to understand the patterns of nature, science was also developing in a different direction. In 1712 the French mathematician, inventor, and naturalist René-Antoine Ferchault de Réaumur (see the sidebar on page 55) demonstrated that crustaceans are able to regenerate lost limbs. He also proved that coral polyps are animals

## RENÉ-ANTOINE FERCHAULT DE RÉAUMUR (1683–1757), AND EXPERIMENTS WITH NATURE

René-Antoine Ferchault de Réaumur was born on February 28, 1683, at La Rochelle, in western France, where his family were landowners and minor nobility. Throughout his life Réaumur was a wealthy man. His education began in La Rochelle and continued at a Jesuit college in Poitiers, where he studied philosophy. In 1699 Réaumur went to Bourges, where he lived under the charge of an uncle, who was a canon of La Sainte-Chapelle, while he studied civil law and mathematics. The family intended him to become a lawyer, but his interest in science prevailed, and in 1703 he moved to Paris, where he continued studying mathematics and began learning physics. Especially interested in geometry, in 1708 he submitted a paper on a general problem in geometry to the Academy of Sciences, as a result of which he was elected a member. He was then 24 years old. In 1710 the government appointed him to oversee the compilation of a description of the useful skills and manufactures in the whole of France. Published after his death in many volumes, his *Description des arts et métiers* (Description of skills and trades) led to the establishment of new industries and the revival of old ones. Discoveries he made concerning iron and steel led to the academy awarding him an annual pension of 12,000 livres, but he requested that the academy use the money for experiments on industrial processes. In 1735 family obligations made it necessary for him to accept the post of commander and superintendent of the royal and military order of Saint-Louis. He performed the duties of his office meticulously, but refused the salary. He was made an honorary member of the Russian Academy of Sciences in 1737 and a fellow of the Royal Society in 1738.

The list of Réaumur's achievements is long. He invented spun glass fibers in 1713; these are now used in fiber optics. In 1719 he suggested that paper could be made from wood—at the time all paper was made from cloth. He invented the cupola furnace for smelting iron in 1720. In 1731 he became interested in meteorology and invented a temperature scale that bears his name (in which water freezes at 0°R and boils at 80°R). He invented an opaque form of porcelain in 1740, and in 1750 he invented an egg incubator.

Above all, Réaumur was a naturalist. He brought to natural history the attitude with which he approached all scientific matters: a strong emphasis on observation; accurate description; and experimentation. In particular, he was one of the first scientists to insist that experiments must be repeated if they are to lead to reliable conclusions. He demonstrated in 1712 that crustaceans are able to regenerate lost limbs, and he proved that corals are animals and not plants. His studies of honeybees allowed him to estimate the number of insects and eggs in a hive, to measure the temperature at which bees hibernate, and he conducted experiments on the geometrical shape of the cells. Barely a year passed without a paper by Réaumur appearing in the *Mémoires de l'Académie des Sciences*

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(Records of the Academy of Sciences), but his most famous written work was *Mémoires pour servir à l'histoire des insectes* (Records to serve as a history of insects), consisting of six volumes published in Amsterdam between 1734 and 1742. Based on Réaumur's close and patient observation, it described the appearance, behavior, and habitat of every insect known at the time, except for beetles.

Réaumur owned several country residences and spent much of his time living in them. On October 17, 1757, while out riding near La Bermondière, his house near St-Julien-du-Terroux, Réaumur fell from his horse, sustaining injuries from which he died the following day.

and not plants, and he studied the lives and behavior of honeybees. Réaumur was a keen observer, as were other naturalists, but he was also an experimenter, and the first to insist that experiments must be replicated if they are to lead to reliable conclusions. He emphasized rigor in observation, meticulous record keeping, and precise experimental procedure. Charles Bonnet (*see* the sidebar "Charles Bonnet (1720–93) and the Discovery of Parthenogenesis" on page 50) was one of Réaumur's students and learned these disciplines from him.

The rise in experimentation made the need for an agreed system of nomenclature even more urgent. Scientists had to know what to call the organisms they collected and used in their experiments if they were to communicate their results to their colleagues. Replication, demanded by Réaumur, was possible only if experimenters knew for certain that they were all dealing with the same organisms.

That system began to appear in 1735, when Carl Linnaeus (1707–78), a Swedish medical student and botanist, published in the Netherlands an 11-page pamphlet with the title *Systema Naturae* (Natural system) containing the beginning of an approach to classification. Carolus Linnaeus was deeply religious and a natural theologian. In the preface to a later edition of *Systema Naturae,* he wrote: "*Creatonis telluris est gloria Dei ex opere Naturae per Hominem solum*" (The Earth's creation is the glory of God, as seen from the works of Nature by Man alone). He also said of himself "*Deus creavit, Linnaeus disposuit*" (God creates, Linnaeus arranges). By the time *Systema Naturae* reached its 10th edition in 1758, it appeared as two volumes and listed 4,400 species of animals and 7,700 species of plants. Twelve editions of the work appeared during Linnaeus's lifetime.

In 1737 Linnaeus published *Genera plantarum* (Plant genera), allocating plants to genera. He developed a plan laid out in 1694 in *Éléments de botanique, ou méthode pour reconnaître les plantes* (Elements of botany, or method for recognizing plants), a book by the French botanist Joseph Pitton de Tournefort (1656–1708). Tournefort made a clear distinction between genera and species, placing about 7,000 plants into 700 genera. He based his classification on fruiting structures, which he considered to be primary, and other features of plants, which he considered secondary. Linnaeus recognized only Tournefort's primary structures in his system, but his work described 935 genera. The sixth and last edition of *Genera plantarum* appeared in 1764.

Linnaeus followed *Genera plantarum* with *Species plantarum* (Plant species), published in two volumes in 1753. It contained descriptions of 6,000 species of plants sent to Linnaeus from every part of the known world. It is still the basic reference work—the starting point—for plant classification.

When Linnaeus began to develop his system, naturalists listed the distinguishing features of organisms, usually in Latin, rather than naming them. This led to long, complicated descriptions that were difficult to remember. Linnaeus replaced this by arranging organisms hierarchically. First he distinguished three kingdoms: Animalia (animals); Vegetabilia (plants); and Mineralia (minerals). He divided each kingdom into classes, the classes into orders, the orders into genera (singular genus), and the genera into species. He sometimes added a category below that of species, but did not name it; today it would be a subspecies or variety. (The rank of phylum, formerly called a division in plants, was added later between kingdom and class.) In Linnaeus's system only two names were needed to identify the great majority of organisms. The first name, conventionally spelled with an initial capital, denoted the genus and the second the species or trivial name. According to the Linnaean system, for instance, the dog rose is *Rosa canina* and the tomato *Lycopersicon esculentum.* Linnaeus named many species himself, and this is often recognized by adding L. or Linn. after the formal name. Many other biologists have named species, of course, and their names are also recognized. The dog rose is *Rosa canina* L. and the tomato *Lycopersicon esculentum* Mill. (for Philip Miller, 1691–1771). This method of naming is called the binomial (two-name) nomenclature. The French anatomist and herbalist Gaspard Bauhin (1550–1624) had used the binomial system earlier, in his work *Pinax theatri botanici* (Illustrated exposition of plants), published in 1623, but Linnaeus developed and popularized the system. Humans, according to Linnaeus, were classified as: kingdom Animalia, class Vertebrata, order Primates, genus *Homo,* species *sapiens—Homo sapiens* L.

In naming plants, Linnaeus relied entirely on the number and arrangement of the reproductive organs. The number of male organs (stamens) determined the class and the number of female organs (pistils) the order. Further distinctions in the arrangement of the organs determined genus and species. Linnaeus was quite open about the sexual emphasis. In 1729 he wrote a thesis for Olof Celsius (1670–1756), his patron, including the following:

> The actual petals of a flower contribute nothing to generation, serving only as the bridal bed which the great Creator has so gloriously prepared, adorned with such precious bed curtains, and perfumed with so many sweet scents in order that the bridegroom and bride may therein celebrate their nuptials with the greater solemnity. When the bed has thus been made ready, then is the time for the bridegroom to embrace his beloved wife and surrender himself to her.

In Linnaeus's own day the sexuality of his system proved controversial. The German botanist Johann Siegesbeck (1686–1755) called it "loathsome harlotry." Linnaeus avenged himself by placing a small European weed in the genus *Siegesbeckia.* Colorful though it was and easy to remember, however, Linnaeus's emphasis on the sexual features of plants was highly misleading because these are not reliable guides to identification. It is not a natural classification because it does not take account of the evolutionary relationships among organisms. Consequently, Linnaeus's original classification did not work very well, and it has been revised many times. What has been retained is the binomial nomenclature that is so helpful in naming organisms.

Carl Linnaeus was born on May 23, 1707, at Råshult, in the province of Småland, in southern Sweden. His father, Nils, was a clergyman. In those days most Swedish people did not have surnames. Instead, they used a patronymic, so Nils had grown up as Nils Ingemarsson—Nils, son of Ingemar—but when he enrolled as a student at Lund University, the authorities required a surname. There was a large linden tree growing on land nearby, so Nils chose the name Linnaeus, a latinized version of *linn,* an old Swedish word for linden (lime) tree. Nils was a clergyman and curate of the village of Stenbrohult, and Råshult was the name of the house Nils had built for his family.

His parents intended that Carl should enter the church, but the boy showed no inclination for that profession. From his earliest years he loved gardening and plants. When he was seven, his parents found a tutor to commence his education, but the man they chose was bad-tempered and surly, and Carl learned little from him. In 1717 he was sent to the lower grammar school in Växjö, about 30 miles (50 km) away. He moved on to the gymnasium (high school) in 1724, but after two years his teachers told his parents that Carl would never become a scholar and was fitted only for manual work. Nils was ill at about that time and went to Växjö to consult Johan Rothman, the state doctor for the province and also a senior teacher at the school. Rothman told Nils that Carl might make a good doctor. He offered to take Carl into his own home and tutor him in botany and physiology for his remaining year at the gymnasium, free of charge. At the end of that year, in August 1727, Linnaeus enrolled at the University of Lund. After a year Rothman advised Linnaeus that he would receive a better medical education at the University of Uppsala, and on August 23, 1728, Linnaeus set off on the 400-mile (644-km) journey north.

One day the poor, shabby, hungry-looking student was sitting in Uppsala University's neglected botanic garden when an elderly clergyman came and sat beside him. The two began talking, and the clergyman asked Linnaeus about the plants they could see. Linnaeus was able to name them and, when asked, told the clergyman that he had a collection of 600 native wild plants. The clergyman asked him to bring them to his house. When he did so, Linnaeus learned he had been talking to Olof Celsius, the professor of theology and dean of the cathedral—and uncle of the astronomer Anders Celsius (1701–44), who devised the temperature scale bearing his name. Realizing that this talented student was poor, Celsius agreed to provide him with lodging and two meals a day. Linnaeus also impressed Olof Rudbeck the Younger (1660–1740), the professor of botany, and in 1730 Rudbeck appointed Linnaeus to give the botanical demonstrations held each spring in the botanic gardens. In gratitude Linnaeus named the genus

*Rudbeckia* in his honor. Linnaeus then began lecturing at the university and went to live in Rudbeck's house, but with Celsius's approval.

On May 12, 1732, Linnaeus embarked on an expedition to Lapland, financed by the Royal Academy of Science. His account of the journey describes many adventures, and one of the most famous portraits of Linnaeus shows him wearing Lapland dress. Linnaeus spent the years from 1735 to 1738 in the Netherlands, where he received his only university degree, in medicine, from the University of Harderwijk. He visited England in 1736, calling on distinguished scientists in London and Oxford, and he spent 1737 studying the garden of George Clifford (1685–1760), a wealthy Dutch banker and keen botanist. Linnaeus collaborated with the German illustrator George Dionysius Ehret (1708–70) in producing *Hortus Cliffortianus* (Clifford's garden), a description of the plants in Clifford's garden, published in 1738. When that was finished, Linnaeus visited Paris before returning to Sweden. In 1739 Linnaeus was a founding member of the Royal Swedish Academy of Sciences.

Back in Sweden, Linnaeus practiced medicine and lectured in Stockholm until, in 1741, he was appointed professor of medicine and botany at Uppsala. Linnaeus expressed his feelings in a letter to a friend, in which he wrote the following:

> By God's grace I am now released from the wretched drudgery of a medical practitioner in Stockholm. I have obtained the position I have coveted for so long: the King has appointed me professor of medicine and botany at Uppsala University and so given me back to botany from which I have been sundered these three years while I was spending my time tending the sick in Stockholm. If life and health are granted to me, you will, I hope, see me accomplish something in botany.

Linnaeus remained at Uppsala for the rest of his life. He revived the botanic garden, arranging the plants according to his new classification. When not teaching, he went on scientific expeditions to various parts of Sweden, taking parties of students with him. Linnaeus also encouraged former students to travel to distant lands in search of specimens to be sent home for him to classify. He called them the apostles and eagerly awaited news from them. Five of the apostles met their deaths on these expeditions, but one of the survivors was Daniel Carl Solander (1733–82), who sailed with James Cook (1728–79) in the *Endeavour* (*see* "Johann Forster, Georg Forster, and James Cook" on pages 69–74).

Carolus Linnaeus, or Carl von Linné (1707–78), was the Swedish naturalist who devised the system for naming species that is still in use today. This picture shows him in about 1770, when he was in his early 60s. *(Hulton Archive)*

In 1757 King Adolf Fredrik (1710–71) made Linnaeus a Knight of the Polar Star. Once his new status had been confirmed, in 1761, Linnaeus began calling himself Carl von Linné. He continued writing and teaching, and his fame spread all over the world. The illustration at right shows him as he looked in about 1770. The order he wears is that of the Polar Star; he was never seen without it.

Linnaeus married Sara Elisabeth (Lisa) Morea in September 1739. They had five daughters and two sons, but one daughter and one son died in infancy. The daughters spent their time with Sara Lisa, who did not enjoy company, and they were poorly educated. Their son, also called Carl von Linné (1741–83) was a botanist and succeeded his father as professor of botany at Uppsala.

In 1758 Linnaeus bought an estate at Hammarby, outside Uppsala, where he used to spend the summers and where he established a museum for his collections. In the 1770s his health deteriorated. He suffered from depression, toothache, and gout, and in 1774 a stroke greatly weakened him. He had a second stroke in 1776, paralyzing his right side. He died on January 10, 1778, during a ceremony in Uppsala cathedral, where he is buried. Following the death of his son Carl in 1783, in order to provide dowries for her daughters, Linnaeus's widow sold his library, manuscripts, and collections to the 24-year-old English medical student and naturalist Sir James Edward Smith (1759–1828), who founded the Linnean Society in London to take care of them. The first meeting of the Linnean Society was held in Smith's home on April 18, 1788.

## WHAT IS A SPECIES?

There was one matter on which Linnaeus and his contemporaries were fully agreed. They might quibble about how to classify species, but no one had the slightest doubt about what constituted a species. It was self-evident. Dogs are different from cats, and both dogs and cats are different from oak trees. In the 17th century botanists tended to regard stable varieties of cultivated plants as distinct species, despite these having been produced by deliberate selective breeding, and they might have classed breeds of dogs as separate species; after all, a chihuahua, dachshund, and deerhound are very different in appearance. In the course of the 20th century, however, matters became more complicated, and the definition of the word *species* was called into question.

The ancient Greeks used the word *genus* to describe a group of organisms that shared many features but were not all the same, and the word *species* to describe a group of organisms that were almost identical. They did not restrict the term *species* to living (or once-living) organisms, however, but also applied it to minerals and other inanimate objects. The word is still sometimes used in that sense; minerals and the products of chemical reactions can be referred to as species. Usually, however, the term is now restricted to biological organisms, and species are grouped into genera. Wolves, coyotes, and dingos are varieties of dogs, so they can be described by the genus dog. Within that genus each of these is a separate species. Similarly, lions, tigers, leopards, and domestic cats can all be described as the genus cat, while each type of cat forms a separate species.

Until the 19th century, scientists supposed that species are unchanging. This allowed them to classify species. It was not always simple because individuals vary, but there was no disagreement about the meaning of the word *species.* By the 18th century, naturalists were grouping similar species and genera into higher categories, but it was not until biologists realized that species evolve that it became necessary to look again at the definition, because if one species can gradually change into two different species the species concept must be more fluid than scientists had previously supposed. Charles Darwin (1809–82) found the resulting confusion amusing. "It is really laughable to see what different ideas are prominent in various naturalists' minds when they speak of 'species,'" he wrote. "It all comes, I believe, from trying to define the indefinable."

Nevertheless, biologists persisted, and in modern times the need to prevent the extinction of species has made the matter more urgent. For example, 18th-century naturalists thought that the wolves of eastern North America were distinct from those of Eurasia, and they called the American wolves *Canis lycaon* and the Eurasian wolves *Canis lupus.* Then in the early 20th century American zoologists decided they were all *lupus,* but in the early 21st century Canadian zoologists decided the wolves of western North America are *lupus* but those of the east are different, and the name *lycaon* has been resurrected. Others disagree. So which is correct, and should the eastern wolves receive special protection to prevent their extinction?

Today there are at least 26 definitions of the word *species,* of which just a few are listed here. Possibly the oldest is called the typological species or morphospecies. It comprises organisms that share specified and fixed properties, such as long or short tails.

The most widely used modern definition is that of the biological species, which was introduced in 1942 by the German-American biologist Ernst Mayr (1904–2005). It is a group of organisms that actually or potentially can breed among themselves but are reproductively isolated from all other groups. By reproductive isolation Mayr did not mean physical separation—by an ocean or mountain range, for instance—so much as biological differences, such as physical incompatibility. This definition does not apply to organisms that reproduce asexually, however, and it may be impossible to tell whether organisms that do not ordinarily interbreed could do so if they chose. Also, some organisms that are clearly different species can produce hybrids; horses and asses are a familiar example, but lions and tigers can also interbreed, and one of the conservation problems surrounding wolves is that the eastern and western American populations—or species?—are known to be interbreeding where their ranges overlap. Wolves and coyotes also interbreed, and both interbreed with domestic dogs. The concept of a biological species allows for a limited number of exceptions because such matings are uncommon, and in many cases the hybrid offspring are infertile.

A microspecies is a group of plants that are genetically uniform. The plants are descended vegetatively from a single parent and are distinct in appearance from other groups derived from the same parent.

A morphological species consists of organisms that look different from other organisms. Cats look different from dogs, for instance, and robins look different from eagles. The idea is simple, but it quickly breaks down. Slow worms have no legs and look very much like snakes, but they are really lizards and distinguished from snakes by their possession of eyelids and visible (though very small) ears, and by their dentition.

A phylogenetic or evolutionary species consists of organisms that share distinguishing features they have inherited from a common ancestor. If populations within such a species diverge in form, they are classed as different species.

A genetic species is a group of organisms that share similar genes.

An ecological species is a group of similar organisms that are united by the environment in which they occur, the climatic range they tolerate, the prey on which they feed, and the predators that hunt them.

There is no sign of an agreed definition emerging any time soon, and it may be that there can be no single definition to suit all purposes. Eventually, therefore, biologists may apply the definition that is best for the organism they wish to identify.

4

# Geography of Living Things

During the 18th century, European nations were busily exploring the world in search of raw materials for their industries and markets for their manufactures. Securing these usually involved claiming the territories where they occurred, and the staking of territorial claims led to the growth of European empires. This merely accelerated a process that had commenced much earlier, which had side effects that may have appeared incidental to the colonial rulers, but that proved to be extremely important in advancing scientific understanding of plant and animal communities because it became the custom for naval surveying ships to carry naturalists, often traveling at their own expense.

The captains of surveying ships were charged with two tasks. The first was to chart newly discovered coastlines, marking hazards to shipping and identifying safe anchorages. The second was to explore the natural resources of the lands along these coasts and for some distance inland. Governments back home needed to know what plants and animals of potential commercial use there were and the ease and convenience with which visiting ships could be provisioned. What happened was that the surveying expeditions attracted some of the most brilliant naturalists, who collected many thousands of specimens, which they drew, described, preserved, and cataloged for later study. The specimens were returned to Europe, where they found their way into collections that later became museums or, in the case of living plants, into botanical gardens and the private gardens of wealthy landowners.

Exploration accompanied by meticulous collecting and naming of species led to a new scientific discipline: *biogeography,* the study of the geographic distribution of plants and animals. This chapter outlines the beginning of biogeography and describes the lives and work of a few of the most prominent contributors to its development.

## EDEN, NOAH, AND MIGRATION

Cornwall occupies the westernmost part of the peninsula of southwestern England, a region of upland moors, dramatically high sea cliffs, and small coves with sandy beaches. It has been a popular tourist destination for many years, but traditionally its economy was based on three industries: agriculture, fishing, and mining for metals such as tin and copper, and for kaolin or china clay, which has many industrial uses—the paper in this book is whitened with kaolin. China clay extraction produces a strange landscape of deep open pits, white hills of waste, and lakes filled with turquoise process water. In the 1990s work began to construct a unique kind of botanical garden in one abandoned Cornish pit. The project involved growing the plants found in an Asian tropical rain forest, including full-size trees, inside a series of vast domes, and recreating desert and temperate plant communities as well as other displays outside. They called the result the Eden Project, and every day it is packed with visitors.

The name was chosen carefully because the Eden Project aims to display the natural world in a pristine state. People are not excluded. All the displays include plants that are exploited for food and fiber, and the rain forest has one or two huts and gardens. People are there, but they live in harmony with their environment. This does not mean the human inhabitants do not modify Eden. Indeed, since the concept derives originally from the Book of Genesis, it is appropriate to point out that Adam was enjoined to manage the garden: "And the Lord God took the man, and put him into the garden of Eden to dress it and to keep it" (Genesis, ii, 15).

Eden, or paradise, is a garden with trees, flowers, and water. It is a perfect place, and in the Middle Ages convent and monastery gardens, where the religious spent time in tranquil contemplation, were often called paradise. Historically, the design and cultivation of European and Middle Eastern gardens was partly an attempt to reflect or recreate the perfection of Eden. John Evelyn (*see* "John Evelyn and Forestry" on pages 20–23) visited Hampton Court, a royal residence near London, on June 9, 1662, and in his description of the palace and its grounds he noted "a parterre [level area] which they call Paradise, in which is a pretty banqueting house set over a cave, or cellar."

Naturalists, however, were becoming aware of a problem. Eden contained representatives of every species, but the biblical flood destroyed all of them except for the breeding pairs that survived aboard Noah's ark. Clearly, therefore, prior to the flood the species must have spread from Eden to all parts of the world. They then perished, but the world was later recolonized by the descendants of those Noah had saved. As the naturalists accumulated specimens and descriptions of more and more species, however, the number of those that must have been accommodated on the ark grew and grew. How big can the ark possibly have been? How did the pairs of sheep, cattle, and deer manage to avoid being eaten by the pairs of hungry wolves, lions, and tigers? Questions also arose over how the postdiluvian survivors could have reached the Americas, Australia, and New Zealand from Mount Ararat, in modern Turkey, where the ark was traditionally believed to have come to rest.

Some animals undertake migrations. Apart from the lemmings of the far north, however, no European mammal travels seasonally in the vast numbers seen in the wildebeest migrations of the African plains or the North American caribou. In Europe birds are the most obvious migrants because they gather in large numbers and depart together. Gilbert White (*see* "Gilbert White and His Letters to Naturalists" on pages 1–11) watched swallows, house martins, and other species migrate and recorded the date of their spring arrival, but even then he had doubts. In his letter of November 4, 1767, to Thomas Pennant, White wrote the following:

> An observing gentleman in London writes me word that he saw a house-martin, on the twenty-third of last October, flying in and out of its nest in the Borough. And I myself, on the twenty-ninth of last October (as I was travelling through Oxford), saw four or five swallows hovering round and settling on the roof of the county-hospital.

> Now is it likely that these poor little birds (which perhaps had not been hatched but a few weeks) should, at that late season of the year, and from so midland a county, attempt a voyage to Goree or Senegal, almost as far as the equator?
>
> I acquiesce entirely in your opinion—that, though most of the swallow kind may migrate, yet some do stay behind and hide with us during the winter.
>
> ---
>
> [Note: Goree is an island off the coast of Senegal in West Africa.]

There was a traditional and persistent belief that swallows, or at least some of them, hibernate. In fact, small though the birds are, swallows nevertheless spend the summer in northern Europe and the winter in Africa south of the Sahara and in India, flying up to 200 miles (320 km) a day on their migrations. They do not hibernate.

Records maintained over a number of years also revealed that conditions change with time, even in quite small areas. Lakes slowly fill with silt, providing a substrate for reeds and other plants that grow in shallow water. The plants trap still more silt, raising the bed until eventually what was once a lake becomes dry land. Obviously the plant and animal communities also change, from which it follows not only that plants and animals are capable of moving from place to place, but that they are sometimes obliged to do so in order to find suitable living conditions. The world cannot be as static as many naturalists believed it to be.

There was also a second problem. Many of the specimens that explorers sent back to Europe were unknown to Europeans. Until examples or eyewitness accounts and drawings by reputable persons reached them, no European naturalist had ever seen a cactus or kangaroo—or, for that matter, a potato, tomato, bell pepper, ear of corn (maize), or any other of the many fruits and vegetables brought from the New World. Evidently different regions of the world supported quite different populations of plants and animals. It was a matter Gilbert White puzzled over. On May 29, 1769, one of his letters included the following:

> The question that you put with regard to those genera of animals that are peculiar to America, viz. how they came there, and whence?

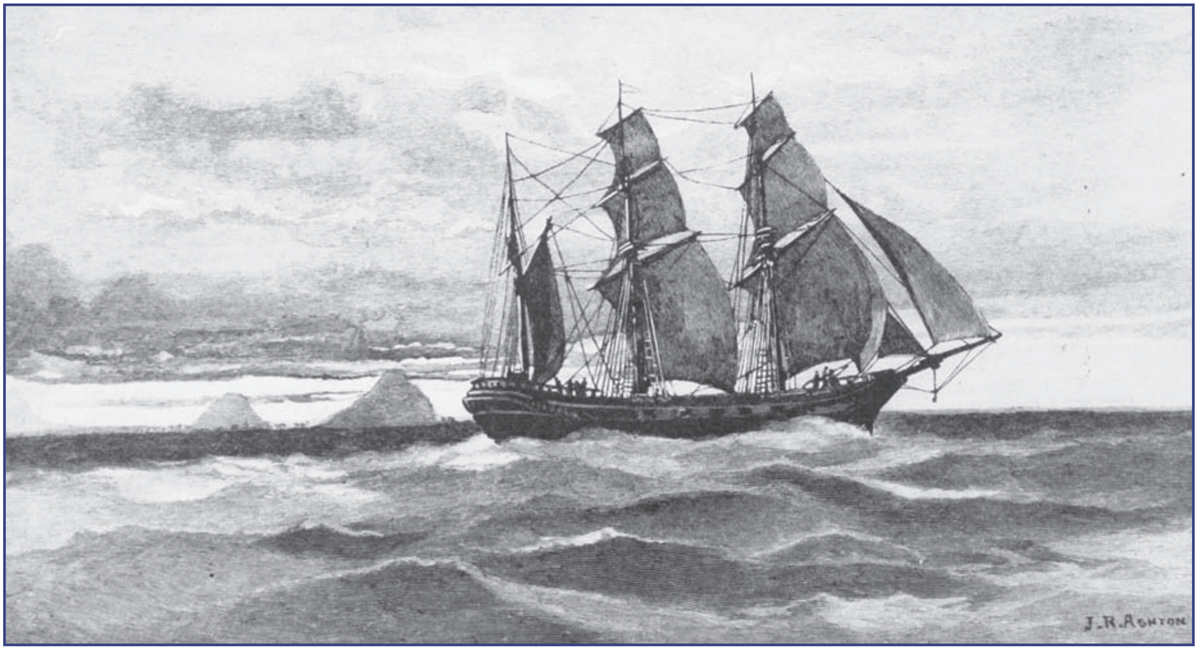
is too puzzling for me to answer; and yet so obvious as often to have struck me with wonder.

White dismissed as ludicrous the idea that at one time a land bridge 3,000 miles (5,000 km) long had spanned the Atlantic, providing a route by which animals—and plants?—could colonize America, only those "peculiar to America" making the journey and leaving none of their kind behind. Linnaeus (*see* "Linnaeus and Binomial Nomenclature" on pages 54–61) had an ingenious solution. He believed, along with many scientists of his day, that at one time a single ocean had covered the entire Earth. In his dissertation "On the Increase of the Habitable Earth" published in 1744, Linnaeus proposed that God might have created all the species in one place that lay above the waters. Then, as the sea receded, species moved out from their island refuge to establish themselves on the newly exposed land. The original area, Linnaeus suggested, must have been in the Tropics to provide habitats suitable for tropical species, but it must have had mountains high enough to provide temperate and arctic habitats.

Linnaeus may have overlooked certain problems his idea left unresolved. Why should the species have migrated? How would temperate and arctic species have fared as they cross the Tropics in search of the climates that suited them—and how did they know such regions awaited them? Why are certain species found only in particular continents and islands if all species originated in the same place? In truth, the difficulties with Linnaeus's hypothesis cannot be resolved. Others proposed a more radical solution: that the plants, animals, and peoples of the Americas had been created separately from the creation that populated the Old World and had escaped the flood. But were the Australasian species also created separately? While the naturalists back home debated these weighty matters, skilled navigators accompanied by other naturalists were exploring the world and beginning to chart the global distribution of species.

## JOHANN FORSTER, GEORG FORSTER, JAMES COOK, AND VOYAGES OF BIOLOGICAL EXPLORATION

On July 13, 1772, James Cook (1728–79) sailed from Plymouth, in the southwest of England, in command of HMS *Resolution,* shown in



HMS *Resolution,* the converted collier in which James Cook explored the islands of the South Pacific and searched for a southern continent *(Time Life Pictures/ Mansell/Getty Images)*

the illustration, and accompanied by a second ship, HMS *Adventure,* commanded by Tobias Furneaux. Both ships were three-masted, square-rigged, converted colliers that Cook had chosen from the yard at Whitby, Yorkshire, where they were built. He was embarking on his second great voyage of discovery, and he took with him a team of scientists, including Johann Reinhold Forster (1729–98) and Forster's son Georg (1754–94). Johann Forster was the official naturalist to the expedition, and Georg assisted his father and was one of the team's artists.

The purpose of the voyage was to search for a southern continent. Many people (but not Cook) believed that the continents of the Northern Hemisphere must be balanced by a similar amount of land in the Southern Hemisphere. This was an idea that originated in ancient Greece, where philosophers thought that the universe was strictly geometrical and must be symmetrical. Since South America and Africa were too small to balance the northern continents there had to be an undiscovered continent to the south of them.

One person who did believe in the southern continent was Joseph Banks (1743–1820), a wealthy naturalist who had accompanied Cook on his first voyage, taking with him his servants and assistants, and paying about £10,000—equal to more than £1 million ($1.5 million) in today's money—for their food and accommodation. Banks had wished to accompany Cook on his second voyage, this time taking with him 16 servants, artists, naturalists, and even two musicians. He demanded that Cook give up his own cabin and live in accommodation provided by a new upper deck. Cook appeared to agree, knowing that the addition of an upper deck would render the ship unseaworthy and that the Admiralty would not sanction the modification. He was correct, and when Banks threatened to withdraw from the mission, taking all his staff with him, the Admiralty permitted him to do so, appointing the two Forsters in his place. That is how Johann and Georg Forster came to sail to the South Pacific.

Johann Forster was born on October 22, 1729, in what was then the Prussian city of Dirschau (it is now the Polish city of Tczew). His ancestry was partly Scottish, his great-grandfather having departed from Scotland after his property was confiscated during the years 1654–58 when the country formed part of the Protectorate established by Oliver Cromwell (1599–1658). Forster studied theology and natural history at the University of Halle, Germany, and became a minister in the Reformed Church at Nassenhuben (Polish Mokry Dwór), where Johann Georg Adam, his eldest son, was born on November 27, 1754. Forster had eight children, of which seven survived.

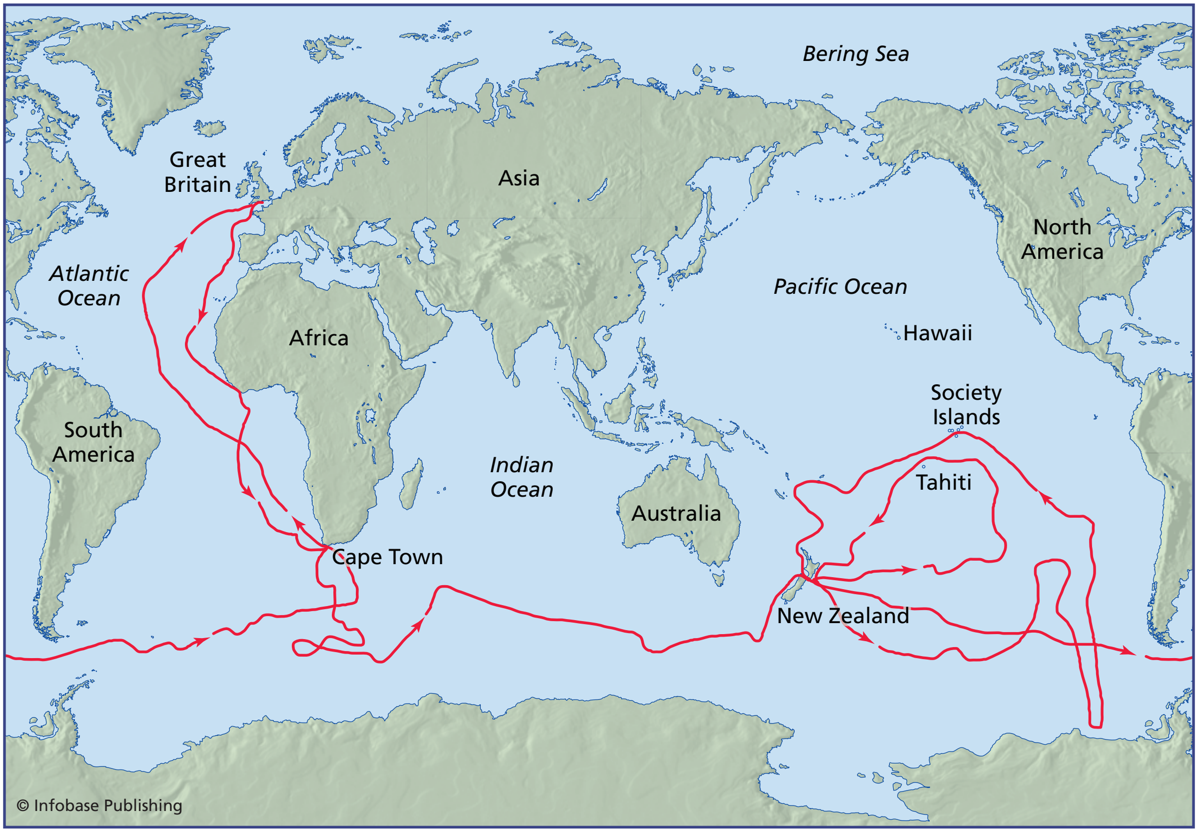
In 1766 Forster moved to England with Georg and spent three years teaching entomology, mineralogy, and other aspects of natural history at the Dissenter's Academy in Warrington, Cheshire. He was dismissed in 1769 for being difficult to work with and moved to London, where he became known among other scientists as an authority on natural history. His growing reputation had brought him to the attention of the earl of Sandwich, the First Lord of the Admiralty, just when Banks was being temperamental.

The Cook expedition headed first to the Cape of Good Hope, and the two Forsters collected specimens and painted pictures of many marine mammals and aquatic birds they saw along the way. Georg, who had been taught by his father, was a skilled naturalist and also a highly talented artist. They spent three weeks at the Cape, studying wildlife that was so abundant and so different from the plant and animals of Europe that Johann persuaded Cook to take on an additional naturalist to help with description and classification. Anders

Sparrman (1748–1820) joined the team, a Swedish physician working in the Cape who was also a former student of Linnaeus. The expedition continued south, encountering the first icebergs on December 10, 1772, and on December 17 both ships crossed the Antarctic Circle; they were the first ships ever to do so. By March 1773, having found no sign of the fabled southern continent, Cook headed for New Zealand. After a brief stop, on June 7 the two ships sailed again, visiting a number of islands and collecting large numbers of natural history specimens. They left Tonga on October 8, and on November 3 Cook arrived back at Queen Charlotte Sound, South Island, New Zealand. The *Adventure* had been delayed, however, and reached Queen Charlotte Sound after Cook had left again. Furneaux returned to England, arriving in July 1774, but Cook made another great sweep of the South Pacific and two more crossings of the Antarctic Circle. On January 30 *Resolution* encountered solid sea ice and thick fog. Cook concluded that the ice extended all the way to the South Pole and in any case it was impossible to continue, so he turned north for the last time. *Resolution* called at more Pacific islands, one of which Cook named New Caledonia, and Cook finally arrived back in England on July 30, 1775. The expedition had lasted three years. The map on page 73 shows the route Cook followed.

Johann Forster was a difficult, disagreeable man, and he had made himself very unpopular with the crew of the *Resolution.* Back on shore, he also succeeded in making himself unpopular with the Admiralty by insisting that it had been agreed that he should write the official account of the voyage. This unlikely claim caused a major row with Cook. As a compromise, the Admiralty agreed that Cook and Forster should collaborate in writing the account, but when that arrangement broke down, the Admiralty backed, and paid for, Cook's own two-volume account, illustrated by 12 charts and 51 engravings, which was published in May 1777. The Forsters published their own account in April 1777, entitled *A Voyage round the World in His Britannic Majesty's Sloop* Resolution, *Commanded by Capt. James Cook, during the Years 1772, 3, 4, and 5,* and in 1778 published another account, *Observations Made During a Voyage Round the World.*

Although Johann's book contained little detailed information about the plants, animals, and peoples they had encountered, it did include an extremely important observation. Forster had noted that within each region of the world the plants and animals formed




James Cook's second voyage took him deep into the sea ice of the Southern Ocean, though not to within sight of Antarctica, but he also visited and charted many islands of the South Pacific.

distinct units, each in its own environment defined mainly by the temperature. As the ship had sailed from the frigid Antarctic to the Tropics, these biological units formed a clearly defined sequence, and the tropical plants and animals were more abundant and more spectacular than those found anywhere else. Forster also recorded that the species living on islands were similar, though not identical, to those found on the nearest continent, but that Asian and American species mingled on some Pacific islands. Forster had discovered the existence of biological provinces. It was the beginning of biogeography.

Having lost the backing of the Admiralty, the Forsters had published at their own expense, but sales of his book failed to bring in enough income to clear the debts Johann had incurred, and most of Georg's paintings had to be sold to Joseph Banks. In November 1779 Johann was appointed professor of natural history and mineralogy at the University of Halle, where he remained until his death on December 9, 1798.

*Voyage Round the World,* on the other hand, contained detailed and perceptive descriptions of the customs and languages of the peoples they had encountered. The book established Georg's scientific reputation, and he was elected to the Royal Society in 1777, at the age of 22. He is sometimes described as the founder of travel literature. Georg Forster died from a stroke in Paris on January 10, 1794, aged 39.

## THE COMTE DE BUFFON AND GEOGRAPHIC ISOLATION

Linnaeus defined species as fixed entities that formed components in a divine plan. He had seen new species appearing in his garden through the hybridization of other species, so he knew that species could change, but he drew from this the conclusion that originally God had created just one species in each genus and that all later species resulted from hybridization among those first species. This did not allow the possibility of entirely new species appearing. What seemed to be new species were merely rearrangements of the characteristics present in the forms God had created.

Not all naturalists agreed with Linnaeus, and his most outspoken critic was Georges-Louis Leclerc, comte de Buffon (1707–88). Buffon saw species within their environmental context. He did not believe in evolution in the modern sense, but he did believe that similar species such as the lion and tiger or ass and horse were descended from a common ancestor, rather than varieties of the same species, and that the differences between them resulted from prolonged geographic isolation.

Buffon had a theory about the origin of the Earth that took account of the fossils of mammoths and mastodons that had been discovered in northern Eurasia. He proposed that a comet had collided with the Sun, striking a glancing blow that had thrown off incandescent material that condensed to form the planets. Each planet cooled at a different rate, and to calculate how long it took for the Earth to cool Buffon heated a metal sphere to white heat and timed how long it took before he could place his hand on it without being burned. From this he figured that the Earth must be at least 70,000 years old. As soon as the temperature was low enough, rain deposited enough water to cover most of the planet in a single ocean almost at boiling temperature. Erosion then altered the surface and produced sedimentary rocks. Animals appeared in the hot oceans, but died when the water temperature fell below the level they could tolerate. Eventually dry land appeared, and animals emerged to inhabit it. These animals developed spontaneously from nonliving matter.

Believing that the polar regions cooled faster than the equatorial region, Buffon suggested that life appeared first around the North and South Poles, as soon as they had cooled sufficiently. As the temperature continued to fall, the polar animals were forced to migrate to lower latitudes and their forms changed. Indian and African elephants were the descendants of mammoths and mastodons that had migrated south, and hippopotamuses were also descended from much larger ancestors that had lived in the far north. As animals migrated, it sometimes happened that sections of the Earth's surface collapsed, isolating them. That, according to Buffon, is how the Old and New Worlds came to be separated.

The physical changes animals underwent were due to the environmental conditions in which they found themselves, and different environments produced different changes. In some places conditions were so unfavorable the migrants died out. Elephants could not tolerate American conditions, for instance, so America has no native elephants. Buffon thought the American climate was generally inhospitable and that American species were smaller than those of the Old World as a result. He knew there were species that occurred only in America, and he thought these might be degenerate descendants of species that had crossed the Atlantic over a land bridge. Unsurprisingly, American naturalists disagreed with his suggestion that America was environmentally inferior to Europe and its species degenerate versions of their Eurasian ancestors.

Buffon was wrong at every point—mammoths and mastodons were not the ancestors of elephants and the planets were not formed by a cometary collision with the Sun—but he had proposed that Earth has a history and so do its species. Animals migrated in search of hospitable environments. In the process some died out in one place but survived in others, and in each new environment the food animals ate, the water they drank, and the air they breathed would bring about physical changes inside them. Their offspring would inherit these changes and in time would become distinct species.

This is not an evolutionary theory, however. Buffon believed, just as strongly as Linnaeus, that species are fixed. That fixity is maintained by species always breeding true, so offspring always resemble their parents. No one at the time knew just how reproduction worked, but many scientists believed that every female holds within her body a large supply of preformed individuals (*see* "Adaptation and the Great Chain of Being" on pages 48–52). Buffon strongly disagreed. He held that particles in the reproductive systems of males and females somehow united and arranged themselves into the form of a new being in the female's womb. The new being was assembled according to a basic plan or mold for its species, which existed in the female body. When species changed in response to environmental changes, the internal plan was modified, and it was the modified plan that offspring inherited. Buffon's ideas influenced the chevalier de Lamarck (Jean-Baptiste-Pierre-Antoine de Monet, 1744–1829), who suggested that the inheritance by offspring of characteristics parents acquired in their lifetime as environmental adaptations might drive the process of evolution. Buffon and Lamarck both influenced Charles Darwin (1809–82).

Georges-Louis Leclerc was born on September 7, 1707, at Montbard, in Côte d'Or, a region in eastern France. His father, Benjamin-François Leclerc, was a wealthy banker, and in 1717, when Georges-Louis was 10, his mother, Anne-Cristine Marlin, inherited a sum of money that allowed her husband to purchase the lordships of Buffon and Montbard. Anne-Cristine also inherited an estate at Buffon, and Benjamin-François added de Buffon to his name. The family moved into a bigger and more impressive house in Dijon and occupied an important social position. Georges-Louis was the eldest of five children and on his father's death in 1725 he also took the name de Buffon.

Buffon entered the Jesuit College of Godrans in Dijon in 1717, and in 1723 he began studying law, as his father wished, but it was soon evident that his talent was for mathematics. In 1727 he discovered the binomial theorem, and before long he was corresponding with leading mathematicians. In 1728 he enrolled at the University of Angers to study mathematics, medicine, and botany, but in 1730 he fought a duel and had to flee from Angers. He went to Nantes, where he lived with a young English friend, the duke of Kingston. Buffon, Kingston, and Kingston's tutor Nathaniel Hickman then toured southern France and Italy, reaching Rome in 1732, where Buffon learned that his mother had died, leaving her fortune to him. He returned home, intending to settle on his estate at Montbard. Highly talented and well connected, Buffon was now very rich, and between 1734 and 1740 his mastery of financial affairs allowed him to greatly increase his fortune. He was asked to study the tensile strength of timber by the minister for the navy, who was engaged in refurbishing the French fleet, and he conducted experiments on more than 1,000 samples of wood. Buffon also wrote a paper in which he introduced differential and integral calculus into probability theory. For this he was elected to the Royal Academy of Sciences in 1734.

Portrait of Georges-Louis Leclerc, comte de Buffon (1707–88) painted by François-Hubert Drouais (1727–75) in 1753 *(Réunion des Musées Nationaux/Art Resource, NY)*

In July 1739 Buffon was appointed keeper of the Jardin du Roi, the royal botanical garden (later called the Jardin des Plantes) in Paris. Over the following years, he enlarged the garden and made it into an important research center and museum. From 1740 his life then fell into a very regular pattern. Every spring he left Paris for his Montbard estate, spending the summer managing the estates, researching, and writing. He returned to Paris each fall and spent the winter working at the botanical garden.

Buffon wrote on a wide range of topics, including mathematics, probability, Earth sciences, astronomy, and physics, but his most famous work was on natural history. He intended his *Histoire naturelle, générale et particulière* to fill 50 volumes and to cover every branch of natural history, geology, and anthropology. He succeeded in completing 36 volumes before he died, and four more were completed after his death by the naturalist the comte de Lacépède (1756–1825), who succeeded him as keeper of the Jardin du Roi.

In 1752 Buffon married Françoise de Saint-Belin-Malain (1732–69). The portrait above right shows Buffon as he was in 1753. They had one son. Buffon hoped his son would become an eminent scientist, but it was not to be. The son turned into a spendthrift and waster, and he was executed in 1794, during the Terror that followed the French Revolution. Buffon was made a count (*comte*) in 1771. He died in Paris on April 16, 1788.

## KARL WILLDENOW AND PLANT DISTRIBUTION

By the end of the 18th century, most of the world's major cities possessed botanical gardens. Berlin also had one, and in 1801 a new director, Professor Karl Willdenow, was appointed to manage it. The garden had been neglected for some time, and in restoring it Willdenow also made a very significant change. Botanical gardens had existed since the 16th century, and their purpose had always been entirely educational. Students and members of the public used them to learn how to identify plants and to discover how plants were classified. To make this easier, the plants were always grouped, so that plants of a particular type, or plants that were in some way related, grew in the same or adjacent beds. These were called *order beds.* Medicinal plants might grow in one part of the garden, for instance, culinary herbs in another, and fiber plants in yet another. With the growing interest in plant classification during the 18th century, it became fashionable to group plants taxonomically. At first the order beds used criteria such as the types of fruits the plants produced, or the structure of their flowers, but as Linnaeus's classification system became more widely known the order beds came to be arranged taxonomically.

When Willdenow took it in hand, the Berlin Botanical Garden was no exception. Its design was based on order beds, and that is what Willdenow changed. He had the garden replanted, this time grouping the plants according to the part of the world and the type of habitat where they were found. Plant collectors sent him specimens from all over the world, so he had no need to travel personally, but he accumulated a large *herbarium*—a collection of dried and pressed plants, identified taxonomically and with information about when and where they were gathered. The garden purchased his herbarium in 1818, after his death. In 1807 Alexander von Humboldt (*see* "Alexander von Humboldt and Aimé Bonpland, Exploring South America" on pages 79–84) helped obtain funding for Willdenow to expand the garden. The Berlin Botanical Garden is still there in the district of Dahlem, and it is open to the public. The garden occupies 106 acres (43 hectares), with 65,000 square feet (6,000 $m^2$) under glass, and it grows approximately 22,000 species of plants. There is also a botanical museum.

Karl Ludwig Willdenow (1765–1812) was interested in the geographic distribution of plants. Johann Forster (*see* "Johann Forster, Georg Forster, James Cook, and Voyages of Biological Exploration" on pages 69–74) had recognized that distinctive plant communities were found in geographic regions defined mainly by temperature, but his descriptions of these included the peoples of those regions and his anthropological theories about them. Willdenow concerned himself exclusively with plants. In 1792 he published his most important work, entitled *Grundriss der Kraüterkunde zu Vorlesungen* (translated into English and published in 1805 as *Principles of Botany*), a book in which he laid the foundation of biogeography. It was Willdenow who inspired Humboldt. The two met in 1788, while Willdenow was still a student, and later Humboldt sent him large amounts of material collected on his travels in South America.

Willdenow was born in Berlin on August 22, 1765. His father was an apothecary (druggist), and Willdenow studied pharmacy at Wieglieb College in Bad Langensalza, Thuringia, graduating in 1785 and then enrolling at the University of Halle, where he studied medicine and botany. He graduated in medicine in 1789, and the following year he took over his father's apothecary business. In the 18th century apothecaries were not quite like modern druggists. They were rivals to physicians, prescribing herbal treatments to patients who came directly to them, preferring the apothecary's medicines to the bleeding and leaching they could expect from a physician. Willdenow worked as an apothecary until 1798, but combined this with his continuing study of plants and their distribution. He published the German edition of *Principles of Botany* during this period, and in 1794 he became a member of the Berlin Academy of Sciences. In 1798 he was appointed professor of natural history at the Berlin Medical-Surgical College, and in 1810 he was made professor of botany at the University of Berlin. In 1801, the year he became director of the botanical garden, he was appointed principal botanist to the Berlin Academy of Sciences. Willdenow remained director of the botanical garden until his death in Berlin on July 10, 1812.

## ALEXANDER VON HUMBOLDT AND AIMÉ BONPLAND, EXPLORING SOUTH AMERICA

Alexander von Humboldt (1769–1859) was 19 in 1788, when he first met Karl Willdenow. At the time, Willdenow was studying medicine, which included studying botany, not with the intention of practicing it, but in order to become an apothecary. Willdenow's interest in plants and their geographic distribution inspired Humboldt, who was about to enroll as a student at the University of Göttingen, Germany, to explore the natural world. In his most famous work, *Kosmos,* published in five volumes between 1845 and 1862, Humboldt wrote that: "I always wanted . . . to understand nature as a whole . . . the separate branches of natural knowledge have a real and intimate connection."

Humboldt's exploration of South America, accompanied by the French botanist Aimé Bonpland (1773–1858), did much to establish biogeography as a distinct scientific discipline, but Humboldt was also an Earth scientist. He invented a miner's safety lamp and founded a school of mining; he studied the volcanoes in the Andes, noting that they lie in straight lines and establishing that this was because they lay above a major fault in the rocks below; he mapped the Earth's magnetic field during his travels, finding the field strongest near the poles and weakest at the equator; he discovered the magnetic equator; and he discovered and measured the Peru Current, which was initially called the Humboldt Current. Humboldt also recorded meteorological data wherever he went.

As though this was not enough for one man, Humboldt was also a diplomat, a staunch opponent of slavery, and a friend of Simón Bolívar (1783–1830), who won freedom from Spanish colonial rule for his own country Venezuela, and then for Colombia, Bolivia, Peru, Ecuador, and Panama. Humboldt became very famous throughout Europe. Indeed, he is said to have been the second most famous man in Europe after Napoleon.

Friedrich Wilhelm Heinrich Alexander, baron (Freiherr) von Humboldt was born in Berlin, Prussia, on September 14, 1769, the son of a major in the Prussian army, who was also the Royal Chamberlain at the Prussian court. Alexander's interest in natural history became evident while he was still a child, and he earned the nickname "little apothecary" for his habit of collecting and labeling plants, insects, and seashells. Their parents hired tutors for Alexander and his elder brother, Wilhelm (1767–1835), until 1789, when Alexander studied economics for a short time at the University of Frankfurt-an-der-Oder, then spent a year at the University of Göttingen. While he was at Göttingen, Alexander developed his interest in natural science, especially geology and mineralogy, and it was while he was a student at Göttingen that he met Georg Forster (*see* "Johann Forster, Georg

Forster, James Cook, and Voyages of Biological Exploration" on pages 69–74). Forster, 15 years his senior, must have told his young friend about his adventures on Cook's second voyage, and the two planned a tour of their own through Europe. They set off in 1790, following the River Rhine northward through the Netherlands and then crossed to England, where Humboldt was introduced to Sir Joseph Banks (1743–1820). Banks had sailed on Cook's first voyage, and when Humboldt met him he was president of the Royal Society.

Realizing he would not achieve his dream of becoming a scientist unless he received a proper education, in 1791 Humboldt enrolled at the Freiberg School of Mining (now the Technische Universität Bergakademie Freiberg). As well as geology, Humboldt also studied languages, anatomy, and astronomy. He left the School of Mines on February 29, 1792, without taking a degree, and in March he was appointed inspector of mines. He toured the Prussian mines—and invented the safety lamp—and then embarked on a tour of salt mines in several European countries. He was also trusted with a number of diplomatic missions.

Humboldt's mother died in 1796, and he inherited a share of the family's considerable fortune. No longer needing to earn a living, Humboldt was able to indulge his passion for travel. In 1797 he resigned from the government department of mines, and in the company of Aimé Bonpland, whom he had met in Paris, Humboldt went to Madrid, where the Spanish prime minister Mariano de Urquijo supported his application to the king and queen for permission to visit Spain's American colonies. Humboldt and Bonpland sailed from Marseille in 1799. During the next five years, the two companions traveled more than 6,000 miles (9,650 km) on foot, horseback, and in canoes. The map shows the route they followed.

They arrived in Cumaná, New Andalusia (now Venezuela), sailed from there to Caracas, then headed inland, crossing the llanos—a treeless grassy plain—until they reached the Apure River, a tributary of the Orinoco. They hoped to discover whether South America's two great river systems, the Orinoco and Amazon, are linked, so they sailed by canoe up the Orinoco, passing through the tropical rain forest and tormented by mosquitoes and the humid heat. Insects and rain destroyed their food supplies, and they lived on ground-up wild cacao (cocoa) beans, which are exceedingly bitter, and river water. They caught an electric eel (*Electrophorus electricus*), and Hum-


The route Alexander von Humboldt and Aimé Bonpland followed through Central and South America between 1799 and 1804

boldt received an electric shock when he dissected it, then later they encountered Amazon river dolphins (*Inia geoffrensis*). Near the source of the Orinoco, they found the Casiquiare River and followed its course. It led them to the River Negro, which then took them into the Amazon. They had proved that the two systems were linked. They returned to the Orinoco and sailed downstream, arriving back at Cumaná in August 1800, having traveled 1,725 miles (2,775 km).

Back in civilization, both suffered an attack of fever. They spent a short time in Cuba, then in March 1801 they returned to Cartagena, New Granada (Colombia). From there they set off through the Andes, heading for Lima, Peru, but were delayed at Bogotá until September because Bonpland fell sick. By this time they had collected more than 3,000 plant specimens. Farther south they climbed several of the mountains, including Mount Chimborazo, 20,569 feet (6,269 m) high, which was then thought to be the world's highest mountain. They reached 18,893 feet (5,762 m), but both suffered from mountain sickness, which Humboldt recognized was caused by the lack of oxygen. They spent six months in Quito, then descended to the coast, where Humboldt measured the temperature of the water in what is now known as the Peru Current. Humboldt also collected *guano*—accumulated bird droppings—and sent a sample to Europe for chemical analysis.

In 1803 the two companions sailed to Acapulco, New Spain (Mexico), where they spent a year. They visited the United States and were received by President Jefferson, then set sail for France, taking with them a truly vast amount of information. They had measured latitudes and longitudes, studied the Earth's magnetic field, collected meteorological data, and made notes on the social conditions in the countries they visited. They had also gathered approximately 60,000 plant specimens, about 6,000 of which were previously unknown to European botanists. While they were in Quito, Humboldt noted the differences in the types of plants he found growing on mountainsides at different altitudes. With increasing elevation, he found the plants resembled those growing in higher latitudes.

Humboldt lived in Paris from 1804 until 1827, spending his time writing his account of the travels. His *Essay on the Geography of Plants* appeared in 1805, and became volume 5 of his 23-volume *Personal Narrative of Travels to the Equinoctial Regions of the New Continent,* coauthored with Bonpland, the final volume of which was published in 1824. By then his fortune was almost spent, and when Friedrich Wilhelm III demanded his return to the Prussian court with the salaried position of chamberlain, Humboldt was in no position to refuse. He moved to Berlin, where he spent the rest of his life, except for a journey he made in 1829 at the invitation of Tsar Nicholas I to inspect the gold and platinum mines in the Ural Mountains.

Humboldt spent his final years working on *Kosmos,* his greatest masterpiece, which developed from a series of lectures he delivered in Berlin in 1827–28. In it he aimed to bring together all of the sciences in a comprehensive portrait of the Earth. The first two volumes were published between 1845 and 1847, volumes 3 and 4 between 1850 and 1858, and as much of volume 5 as he had been able to complete appeared in 1862, after his death. Humboldt suffered a minor stroke on February 24, 1857, from which he recovered, but his strength weakened during the winter of 1858–59, and he died peacefully on May 6, 1859. He was given a state funeral.

Aimé-Jacques-Alexandre Goujaud was born in La Rochelle, France, on August 28, 1773. He later changed his name to Bonpland. He studied medicine in Paris from 1791 to 1794, served as a surgeon in the French army until 1795, then resumed his medical studies. In 1799 Humboldt chose him as a companion for the exploration of South America and to oversee the botanical collections. On his return to France in 1804, Bonpland was awarded an official pension and made director of the Empress Josephine's private botanical garden at Malmaison, her country house about 7 miles (11 km) from Paris. Installed at Malmaison, he spent much of his time arranging his botanical collections and writing, either as sole author or as Humboldt's coauthor. In 1808 Josephine appointed him her official botanist. In 1813 Bonpland published *Description des Plantes Rares Cultivée à Malmaison et à Navarre* (Description of the rare plants cultivated at Malmaison and Navarre) a book describing the contents of Josephine's garden.

Josephine died in 1814, and Bonpland decided to return to South America. He left France in late 1816 to take up a post as professor of natural sciences in Buenos Aires, Argentina, where he also practiced medicine. In 1817 he was made a corresponding member of the French Académie des Sciences. In 1820 he left Buenos Aires to establish and run a plantation near the Paraná River, but he offended the dictator of Paraguay, who had him detained until 1829. After his release, Bonpland started other plantations in Brazil and Uruguay, which he managed from 1831 until his death. In 1854 Bonpland was decorated by King Friedrich Wilhelm III of Prussia, and in 1856 he received an honorary degree from the University of Greifswald, in Germany. Bonpland died on May 11, 1858, at Restauración, Argentina.

5

# Charles Darwin and His "Entangled Bank"

Charles Darwin (1809–82) published his most famous book in 1859, giving it the full title: *On the Origin of Species by Means of Natural Selection or The Preservation of Favoured Races in the Struggle for Life.* It is most often known as *Origin of Species* or simply *Origin.* Darwin's theory is essentially ecological. That is to say, it proposes that species evolve as a result of the ways they relate to their natural surroundings and to the other species they encounter there, competing with them for food, water, and shelter. Natural selection favors those individuals possessing traits that help them to prosper in the particular circumstances in which they live.

Darwin emphasized the ecological nature of his idea in the final paragraph of his book. The word *ecology* had not yet been coined so he was unable to use it, but the picture he painted of what he called an "entangled bank" is clear. He began his final paragraph with the following sentence:

> It is interesting to contemplate an entangled bank, clothed with many plants of different kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us.

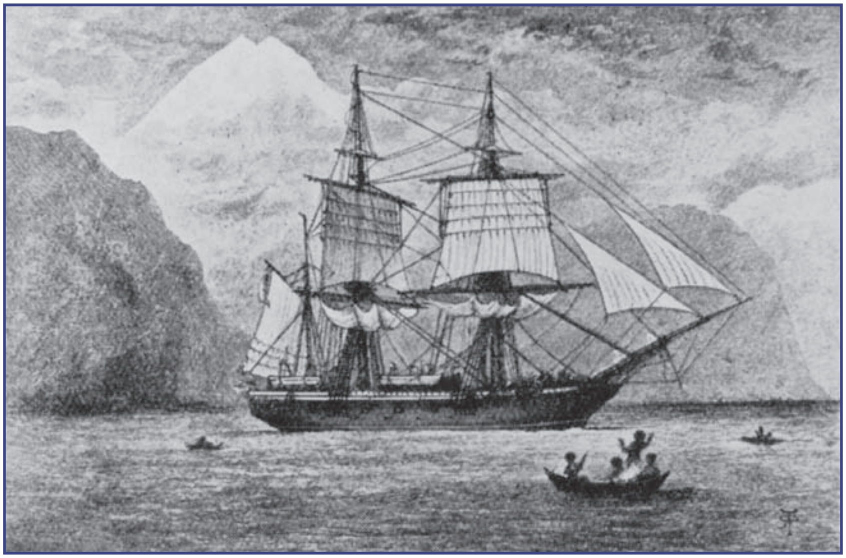
This chapter explores Darwin's theory. It describes how Darwin came to travel the world on HMS *Beagle* and the observations he made that led him to his understanding of the evolutionary process. It explains his theory and how it came to be published. Major scientific advances do not spring suddenly from nowhere. The person who receives the credit usually brings together and puts the finishing touches to thoughts and ideas that have been in circulation for some years. This was certainly true of Darwin, and the fact does nothing to detract from the man's genius, but he was forced to publish because another naturalist, Alfred Russel Wallace (1823–1913), had reached the same conclusion independently.

Having outlined the theory and its origins—the origin of the *Origin,* one might say—the chapter goes on to describe how biologists interpreting the theory of evolution by natural selection developed the central themes of ecology. It explains the work of Thomas Malthus, which strongly influenced Darwin, and of Ernst Haeckel, who invented the word *ecology.* In recent times James Lovelock has applied ecological concepts to the search for life on other planets, then turned them back to suggest that at some level all Earth's living inhabitants collaborate to make Earth a unified living organism. This is known as the Gaia hypothesis, and the chapter explains it.

## DARWIN AND THE *BEAGLE*

On December 27, 1831, HMS *Beagle* set sail from Plymouth under the command of Robert FitzRoy (1805–65). FitzRoy's mission was to continue the survey, commenced some years earlier, of the coasts of Patagonia, Tierra del Fuego, and the Magellan Strait. FitzRoy had already established his reputation as a highly skilled surveyor and seaman. He had ranked first in the final examinations at naval college and had scored full marks—an unprecedented feat—in the examination for promotion to lieutenant. The picture on page 87 shows the *Beagle* in the Magellan Strait.

FitzRoy had commanded the *Beagle* before. On its previous voyage, he had taken over when the ship's previous commander had committed suicide. He knew how stressful and lonely a command could be. In the 19th century, a British naval commander belonged to a different social class from the members of his crew, and there could be no question of any social contact with them. This was the

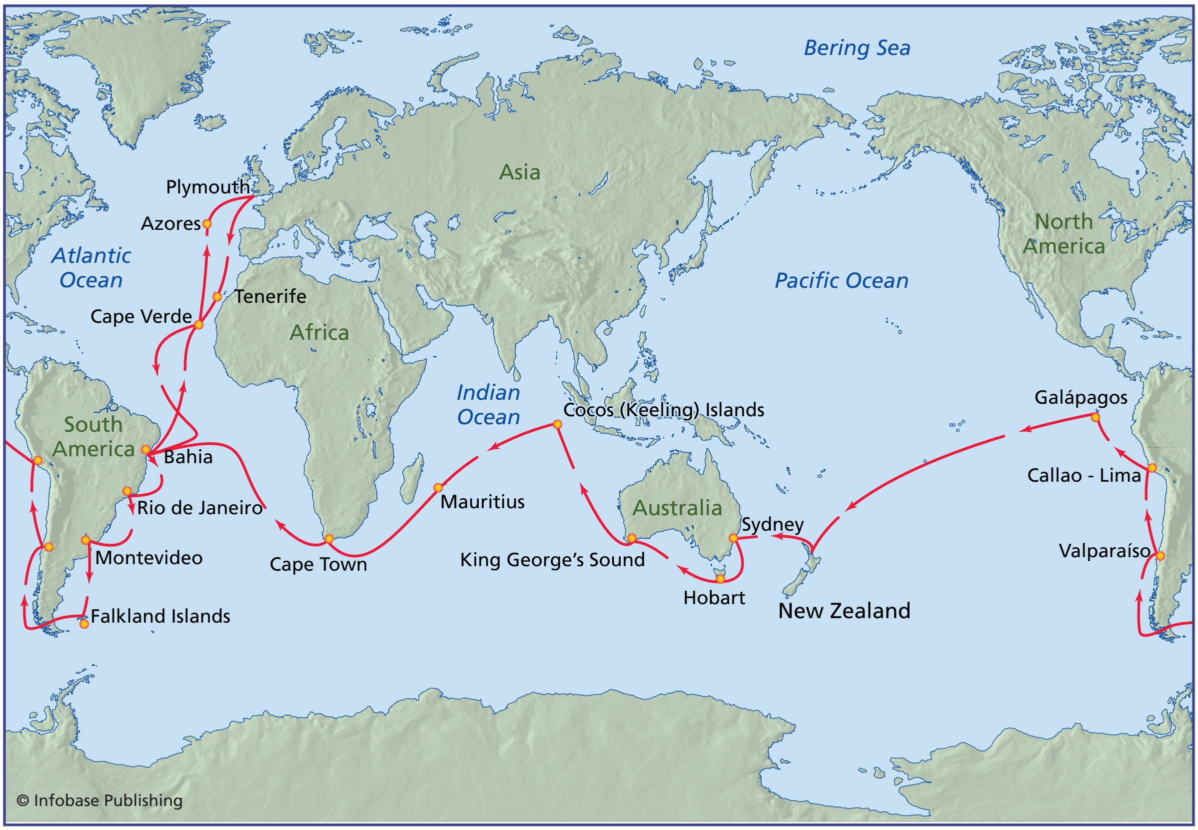


HMS *Beagle* pictured in the Strait of Magellan during her voyage around the world. *Beagle* was a brig-sloop, 90.3 feet (27.5 m) long, 24.5 feet (7.5 m) in the beam, and with a draft of 12.5 feet (3.8 m). She carried a crew of 65 sailors and nine supernumeraries, one of them Charles Darwin. *(Hulton Archive/Getty Images)*

situation every commander faced, but it was especially acute for FitzRoy, who was an aristocrat directly descended from Charles II. As commander he would have to live alone and even eat alone, with no opportunity for pleasant mealtime conversation. So FitzRoy knew he needed a companion. His friend Francis Beaufort (1774–1857), hydrographer to the Admiralty, had helped FitzRoy obtain his command, and FitzRoy asked him to recommend a suitable companion. He asked Beaufort to find "some well-educated and scientific person . . . who would willingly share such accommodation as I have to offer, in order to profit by the opportunity of visiting countries yet little known." In fact the companion would have to sleep in the chart room, on the deck above FitzRoy's cabin. It measured 9 feet by 11 feet (2.7 × 3.4 m) and was nowhere more than 5 feet (1.5 m) high, one of the ship's masts passed through the room, and the chart table, 4 × 6 feet (1.2 × 1.8 m) occupied the center. Bookshelves, storage cabinets, an oven, and washstand stood against the walls. That was to be the companion's home.

Beaufort approached the Rev. Professor John Stevens Henslow (1796–1861), who was one of Darwin's closest friends. Henslow refused the invitation for himself but advised Darwin to apply for the position. Several other people had been approached but had turned FitzRoy down, and on September 5, 1831, Darwin traveled to Plymouth to meet the captain. The two got along well, and they agreed that Darwin would sail with FitzRoy as his gentleman companion. FitzRoy's liking and respect for Darwin led him later to allow Darwin to take over as the ship's naturalist from Robert McCormick, who was combining naturalist with the position of senior ship's surgeon. Darwin did not start as an official member of the crew, however, and he had to provide his own equipment and pay £500 for his passage—equivalent to about £36,000 ($50,000) in today's money.

The map on page 88 shows the route the *Beagle* followed. During the voyage Darwin was a poor sailor. He suffered badly from seasick-




The route of HMS *Beagle* on its five-year voyage around the world, with Charles Darwin sailing as gentleman companion to the commander, Robert FitzRoy ness and spent as much time on land as he could, where possible leaving the ship at one port and joining it again at another, having made the journey between the two over land. He was ill several times and in 1834 had to spend a month in bed.

Robert FitzRoy had a keen interest in the latest scientific ideas, and before they sailed he gave Darwin a copy of the first volume of *Principles of Geology* by Charles Lyell (1797–1875). In this book Lyell maintained that ancient geological features should be explained by reference to processes that are active at the present time and that geological change takes place through the accumulation of countless small changes. The book influenced Darwin profoundly, and he arranged for the second volume to be sent to him as soon as it was published (the book appeared in three volumes published between 1830 and 1833). In his second volume Lyell argued against evolution, proposing instead that species originated in what he called "centers of creation," from where they spread outward.

Lyell had asked FitzRoy to look out for *erratic* boulders whenever he went ashore; an erratic is a rock—boulder or gravel—that has been transported by glacial action and is therefore of a different type from the underlying bedrock. Darwin began noticing rock formations from the first time he stepped ashore in Cape Verde, where he saw a band of white rock high on a volcanic cliff that he identified as coral and shells that had been exposed to intense heat. Later, he found raised beaches, marking places where sea level had fallen. He observed coral atolls and figured out (correctly) how they form. He found the fossils of gigantic mammals that are now extinct, including *Megatherium,* a sloth the size of an elephant. When they reached the Galápagos Islands, Darwin learned that local people could tell which island a native tortoise came from by its appearance. Darwin collected specimens of the small birds he found on the islands. After he returned to England, the ornithologist John Gould (1804–81) recognized that 14 of them were finches that had all descended from the same ancestor—a bird found on the South American mainland—and had changed the size and shape of their bills as they adapted to the food available on each island.

Darwin mailed fossil specimens and reports of his progress to his friend Henslow, who showed them to leading naturalists, so by the time Darwin arrived back in England he was already something of a celebrity in scientific circles. At the same time, Darwin's father, the society doctor and wealthy financier Robert Darwin (1766–1848), had invested so successfully for his son that Charles Darwin was able to live for the rest of his life as a gentleman scientist, with no need to worry about earning a living.

HMS *Beagle* arrived back in England on October 2, 1836, and Darwin hurried home to Shrewsbury, his hometown in Shropshire, to visit his family, arriving late in the evening of October 4. On October 15 he traveled to Cambridge to meet Henslow, who advised him to find naturalists to help him catalog his specimens. That quest took Darwin to London, where he visited the major museums. The *Beagle* sailed from Plymouth to Woolwich, London, arriving on October 29, and Darwin supervised the removal of his crates of material. That evening he met Charles Lyell, who introduced him to Richard Owen (1804–92), an anatomist, paleontologist, and one of the most talented biologists in the country. Owen agreed to examine Darwin's fossils, and later he identified some of the fossil bones Darwin had collected as belonging to *Scelidotherium,* a ground sloth, *Toxodon,* a large rodent, and plates from *Glyptodon,* a giant armadillo.

The next few months Darwin divided his time between Shrewsbury, London, and Cambridge, finally settling in London. On November 1, 1836, he was elected a fellow of the Royal Geological Society. He had given a talk in Cambridge on the formation of glassy tubes by lightning strokes, and on January 4, 1837, in an important lecture to the London Geological Society, Darwin proposed that South America had risen very slowly and the adjacent seabed had subsided. As the land rose, the animals living on it somehow adapted to the gradually changing conditions. It was a sign that Darwin's ideas were developing. Many of the leading geologists attended the lecture and gave it a favorable reception. Darwin was now accepted among the English scientific elite.

## EVOLUTION BY MEANS OF NATURAL SELECTION

Darwin then settled down to work through his ideas and organize the notes he had made while on the *Beagle.* In May 1838 the official account of the voyage was published in four volumes, entitled *Narrative of the Surveying Voyages of His Majesty's Ships* Adventure *and* Beagle. The first volume described the *Beagle*'s first voyage, before FitzRoy took command. The second was FitzRoy's own account of the voyage, and Darwin's *Journal and Remarks 1832–1835* formed the third volume. The final volume was a long index. In 1845 Darwin's volume appeared separately as *Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of HMS* Beagle *Round the World, Under the Command of Capt. FitzRoy, R.N.,* published by John Murray. The book is usually known as *The Voyage of the* Beagle, and it is still in print.

In November 1838 Darwin proposed to his cousin Emma Wedgwood (1808–96), and the delighted family arranged for the couple to receive a dowry and investments that would bring them an annual income of about £2,000, a small fortune worth approximately £140,000 ($200,000) in today's money. They were married on January 29, 1839. In 1842 Charles and Emma Darwin found a suitable house for their family in Kent. It was called Down House, and Charles's father bought it for them.

Darwin was not the only naturalist searching for a way to explain the evolution of species; the idea had been around for many years. In 1809 Jean-Baptiste Lamarck (*see* "The Comte de Buffon and Geographic Isolation" on pages 74–77) had published a book on invertebrate zoology called *Philosophie zoologique* (Zoological science) in which he propounded the idea that characteristics an animal acquired during its lifetime might be transmitted to its offspring. Lamarck's colleague, the professor of zoology at the University of Paris Étienne Geoffroy Saint-Hilaire (1772–1844), believed that all animals have the same basic parts and that if certain parts develop, other parts must decrease in proportion. In his book *Philosophie anatomique* (Anatomical science), published between 1818 and 1822, Geoffroy expounded his view that all vertebrates were modified versions of a single underlying plan. Species could change slowly from generation to generation, but only within the constraints of that essential form. Robert Edmond Grant (1793–1874), professor of comparative anatomy at University College London (UCL), dean of the UCL medical faculty from 1847, and Fullerian Professor of Physiology at the Royal Institution 1837–38, a marine biologist and invertebrate zoologist, was a close friend of Geoffroy, but much more radical, politically and scientifically. He believed species could transmute into other species, and he rejected any notion of supernatural intervention in the process. Darwin had studied under Grant, and they became close friends; it was Grant who first interested Darwin in marine biology. Grant was a controversial figure, however, and although he offered to help, Darwin would not permit him to work on the *Beagle* specimens—consequently, no monograph was ever published on the corals Darwin collected.

The explanation of evolution that Darwin was developing was elegant in its simplicity. Darwin discovered the key to the problem when he read an essay by an economist that was attracting much attention (*see* the sidebar “Thomas Malthus and *An Essay on the Principle of Population* on page 98). In his autobiography Darwin described what happened in the following words:

> In October 1838, that is, fifteen months after I had begun my systematic inquiry, I happened to read for amusement Malthus on *Population,* and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones destroyed. The results of this would be the formation of a new species. Here, then I had at last got a theory by which to work.

The general principles of Darwin’s theory of evolution by means of natural selection are easy to understand:

- Every member of a species is slightly different from all other members; in other words there is variation among the individuals of a species.
- On average, parents produce more offspring than are needed to replace them; in their lifetimes two parents are capable of producing more than two offspring.
- Populations cannot possibly continue to increase indefinitely and, on average, population sizes remain stable.
- The stability of population sizes despite the capacity of populations to increase implies that in every generation there must be competition for survival.
- In that competition, those individuals possessing variations that help them to obtain resources and mates will tend to produce more offspring than other individuals lacking those variations.

- The offspring will inherit their parents' advantageous traits.
- Over many generations, the descendants of the better-adapted individuals will become more numerous.
- As gradual changes in the environment alter the conditions under which species live, different variations among individuals will prove advantageous and nature will select those variations. This natural selection will lead to the emergence of new species.

Darwin worked on his theory, discussing it with close friends, but he was reluctant to publish because he knew it would prove controversial. Nevertheless, by July 1842 he had written a 230-page draft of his theory and the evidence to back it. The illustration at right shows him at about this time, as a serious, deeply thoughtful man in his early 40s.

Still hesitant about publishing, the pressure on him was building. In 1844 the London medical publisher John Churchill brought out a book with the title *Vestiges of the Natural History of Creation,* proposing that everything in the universe, including species of organisms, had arisen from earlier forms. This was evolution, although the book suggested no process by which it might happen, and Darwin thought the book amateurish. The book was published anonymously, and there was much speculation about the identity of its author. The mystery was solved in 1884, when the 12th edition revealed that the author was Robert Chambers (1802–71), a Scottish journalist (and, with his brother William, founder of the publishing company W. and R. Chambers). Chambers's book did not amount to competition, but on the other side of the world another naturalist, A. R. Wallace, had independently arrived at a conclusion much closer to Darwin's.

Charles Darwin (1809–82) in an engraving made in 1851 by T. H. Maguire for the British Museum; Darwin is 42 and had completed the first draft of his evolutionary theory. *(Hulton Archive/Getty Images)*

Alfred Russel Wallace was born on January 8, 1823, at Usk, Monmouthshire, the eighth of nine children. In 1828 the family moved to Hereford, and for some years the father, Thomas Wallace, was town librarian there, but in 1835 Thomas was swindled out of his property, and the family fell on hard times. Alfred had to leave school in December 1836, and he and his brother John went to London. By the middle of 1837 Alfred was training to be a surveyor in his brother William's surveying business, working first in Bedfordshire, then around Hereford, and later at Neath in South Wales. He became increasingly interested in natural history and began attending lectures at meetings of local scientific societies. By 1841 he was giving lectures himself and had started to write essays on natural history topics.

In 1843 William's business experienced difficulties, and Alfred had to leave. He obtained a position as teacher of drafting, surveying, English, and arithmetic at the Collegiate School in Leicester. The school had a good library, and Alfred was able to continue studying natural history. In 1844 he became friendly with Henry Walter Bates (1825–92), a keen entomologist. William Wallace died in February 1845, and Alfred quit his teaching job to run the surveying business, which had recovered from its earlier difficulties. He still found time to maintain his interests in natural history, and he kept in touch with Bates.

Wallace did not enjoy managing the business, and when he read a travel book about the Amazon he saw a way out. He would become a professional naturalist, traveling and collecting specimens he would sell to finance his travels. There was such a demand for exotic plants and animals that collectors could earn a reasonable living this way. Wallace persuaded Bates to join him, and on April 25, 1848, the two young men set off for South America, arriving at Pará (now Belém) at the mouth of the Amazon on May 28. The two separated early in 1850 for reasons that remain unknown, and Wallace continued alone exploring the wildlife of the Amazon and Negro Rivers. Wallace had read *Vestiges of the Natural History of Creation,* and as he gathered specimens he was already seeking an explanation for the evolutionary process the book described.

Wallace had never been strong, and in 1852 his health had deteriorated to the extent that he had to return to England, but on August 6 the ship on which he was sailing caught fire and sank. He lost his collections and with other survivors spent 10 days in a lifeboat before being rescued. His collections had been partly insured, but he was unable to study them back in England or sell specimens from them. He attended meetings, delivered lectures, and wrote two books, *Palm Trees of the Amazon and Their Uses* and *A Narrative of Travels on the Amazon and Río Negro,* but he finally decided to go overseas once more and resume collecting, this time in the Malay Archipelago (Malaysia and Indonesia). He reached Singapore on April 20, 1854, and set to work. He spent eight years among the islands, during which time he undertook approximately 70 expeditions and collected more than 125,000 specimens.

His ideas on evolution continued to form, and in 1855 Wallace set out his theory in a paper with the title "On the Law Which Has Regulated the Introduction of New Species," published in the *Annals and Magazine of Natural History.* Charles Lyell read the paper and showed it to Darwin, but Darwin took little notice of it. In February 1858 Wallace fell sick with malaria while in the Moluccas, and as he lay in bed he made the connection between the essay by Malthus and the method by which evolution must operate. He had been corresponding with Darwin since 1856 and knew that Darwin was thinking along similar lines, so when he recovered Wallace wrote out his version of the theory and sent it to Darwin. He entitled it "On the Tendency of Varieties to Depart Indefinitely From the Original Type."

Darwin received Wallace's paper on June 18, 1858. After reading it, he sent it to Lyell, asking Lyell to return it and saying that although Wallace had not asked him to publish the paper, of course he would write to Wallace at once, offering to send the paper to any journal. Wallace's theory was close to Darwin's, but there were important differences. Wallace appeared to be thinking of varieties or subspecies within a population. He maintained that once varieties or subspecies existed—he did not suggest how they might come to exist—they would compete for resources until only one remained. Darwin based his theory on variations within individuals of the same species.

Nevertheless, the two theories were sufficiently similar that Darwin decided he had to make his own theory known. He had no wish to injure Wallace, however, and it was agreed that Wallace's paper and Darwin's theory should be presented together. The event took place on July 1, 1858, at a meeting in London of the Linnean Society. Wallace was still in Asia, and Darwin was unwell and could not make the journey to London, so Charles Lyell and another of Darwin's friends, the botanist Sir Joseph Dalton Hooker (1817–1911), presented the papers on their behalf. The meeting was given the title "On the Tendency of Species to Form Varieties and Species by Natural Means of Selection" and comprised the following:

- Wallace's paper;
- Two extracts from a manuscript Darwin wrote in 1839: "The Variation of Organic Beings Under Domestication and in Their Natural State" and "On the Variation of Organic Beings in the State of Nature; on the Natural Means of Selection; on the Comparison of Domestic Races and Species";
- Part of a letter Darwin had written to Asa Gray (1810–88), professor of natural history at Harvard University, outlining his theory.

Darwin spent the next few months reducing the length of the book he had been preparing. He passed the finished manuscript to John Murray. On November 2, 1859, Darwin received the first copies of *Origins.*

Wallace returned to England in 1862. He spent time arranging his collections and lecturing, and he visited Darwin at Down House. He became friendly with Charles Lyell and continued corresponding with Darwin on a range of topics. He died at his home at Broadstone, Dorset, on November 7, 1913.

## POPULATION AND RESOURCES

As they worked on their respective versions of a theory of evolution by natural selection, both Darwin and Wallace read a short book—it was little more than a pamphlet—that had made its author a celebrity following its publication in 1798. Its importance lay in its simple, straightforward demonstration of the way resources constrain populations. The book is famous still and has never been out of print. It was written by Thomas Malthus (*see* sidebar on page 98), and its full title was *An Essay on the Principle of Population As It Affects the Future Improvement of Society With Remarks on the Speculations of Mr. Godwin, M. Condorcet, and Other Writers.* It is usually known as *An Essay on the Principle of Population,* but the full title reveals Malthus's original purpose. The portrait on page 97 shows Malthus in 1800, at about the time of its publication.

Malthus was raised in a household dominated by the ideas of the progressive philosophers of the 18th century. His father, Daniel, knew Jean-Jacques Rousseau (1712–88) and David Hume (1711–76) personally. In particular, Daniel Malthus believed that living conditions for working people could be greatly and sustainably improved. That was the view of the English writer and political philosopher William Godwin (1756–1836) and the French philosopher, political scientist, and mathematician Marie-Jean-Antoine-Nicolas de Caritat, marquis de Condorcet (1743–94). Rousseau, Hume, Godwin, and Condorcet were all infected by the euphoria that followed the French Revolution of 1789, which Thomas Malthus described as a "blazing comet." The revolution promised freedom of thought and from that a rapid increase in knowledge that would lead to economic advancement. That in turn would generate rising incomes and prosperity, which, because of the egalitarian ideals of the revolution, would benefit working people. It was a time of huge optimism.

Thomas Robert Malthus (1766–1834) was Britain's first professor of economics and author of *An Essay on the Principle of Population,* which profoundly influenced both Charles Darwin and Alfred Russel Wallace in their development of a theory of evolution by natural selection. This portrait, drawn on January 1, 1800, shows Malthus at the age of 33. *(Pictorial Parade/Getty Images)*

Thomas Malthus had doubts, however. He believed that the prospect of perpetual improvement raised a difficult question, a question he posed in the following words in the first chapter of his *Essay:*

> It has been said that the great question is now at issue, whether man shall henceforth start forwards with accelerated velocity towards illimitable, and hitherto unconceived improvements, or be condemned to a perpetual oscillation between happiness and misery, and after every effort remain still at an immeasurable distance from the wished-for goal.

The question arose because of a disparity between the rate at which a population can increase in size and the rate at which it can be supplied with necessities. He found an example in the rate of population growth in the United States and outlined the problem as follows in the second chapter of the *Essay.*

> In the United States of America, where the means of subsistence have been made more ample, the manners of the people more pure, and consequently the checks to early marriages fewer, than in any of the modern states of Europe, the population has been found to double itself in twenty-five years.

## THOMAS MALTHUS AND *AN ESSAY ON THE PRINCIPLE OF POPULATION*

Thomas Robert Malthus is known today as Thomas Malthus, but he always used his middle name and in his lifetime was known as Robert Malthus. He was born on February 13, 1766, at a country estate called The Rookery, near Dorking, Surrey, to the south of London. He was the second of the eight children (two sons, one older than Robert, and six daughters) of Daniel and Henrietta Malthus. The family was prosperous, and Daniel Malthus, who closely followed the intellectual debates of the day, knew the philosophers Jean-Jacques Rousseau (1712–88) and David Hume (1711–76). Malthus was educated privately by his father and tutors until 1784, when he entered Jesus College, University of Cambridge, to study mathematics. He graduated in 1788, with the equivalent of a first-class honors degree in mathematics, and he was ordained a minister in the Church of England the same year. He received his master's degree in 1791 and was elected a fellow of Jesus College in 1793. While at Cambridge, Malthus also studied English and French literature and won prizes for public speaking (declamation) in Latin and Greek as well as in English, an achievement made more remarkable because he had inherited a cleft lip and cleft palate. His interest in mathematics was largely practical, and he acquired a good understanding of Newtonian physics.

In about 1796 Malthus became a curate in the parish of Albury, Surrey, not far from his family's home, and he divided his time between Albury and Cambridge until 1804, when he married Harriet Eckersall. College fellows must be unmarried, so Malthus had to resign his fellowship. He published the first edition of his most famous work, *An Essay on the Principle of Population,* in 1798. Five further editions appeared between 1803 and 1826, and with each revision Malthus incorporated new material, addressed earlier criticisms, and modified his own views. Publication of the *Essay* made Malthus famous among intellectuals, many of whom reviled him for what they saw as his hard-hearted rejection of any possibility for improving the living conditions of the poor. Their criticisms were directed principally at the first edition of the *Essay,* however; Malthus dealt with them in later editions.

Following the publication of the second edition of the *Essay,* in 1805 Malthus was appointed professor of modern history and political economy at the East India College, recently founded by the East India Company to provide a two-year course of general studies and languages for company employees before they were posted overseas. The college later became Haileybury College, which still exists as an independent school. The appointment made Malthus Britain's first professor of economics—although the economist Adam Smith (1723–90) was made a professor at Glasgow University in 1752, he was professor of moral philosophy, not economics. By all accounts Malthus was a popular teacher, nicknamed "Population Malthus" or just "Pop" by his students. In 1818 he was made a fellow of the Royal Society.

In addition to his pioneering study of population, Malthus researched and wrote on a variety of economic subjects. He was especially interested in the arguments surrounding free trade and protectionism as this affected the price of grain, in rents, and in monetary theory. He died at Bath, Somerset, on December 23, 1834, where he is buried.

> This ratio of increase, though short of the utmost power of population, yet as the result of actual experience, we will take as our rule, and say, that population, when unchecked, goes on doubling itself every twenty-five years or increases in a geometrical ratio.
>
> Let us now take any spot of earth, this Island for instance, and see in what ratio the subsistence it affords can be supposed to increase. We will begin with it under its present state of cultivation.
>
> If I allow that by the best possible policy, by breaking up more land and by great encouragements to agriculture, the produce of this Island may be doubled in the first twenty-five years, I think it will be allowing as much as any person can well demand.
>
> In the next twenty-five years, it is impossible to suppose that the produce could be quadrupled. It would be contrary to all our knowledge of the qualities of land. The very utmost that we can conceive, is, that the increase in the second twenty-five years might equal the present produce. Let us take this for our rule, though certainly far beyond the truth, and allow that, by great exertion, the whole produce of the Island might be increased every twenty-five years, by a quantity of subsistence equal to what it at present produces.
>
> Yet this ratio of increase is evidently arithmetical.

The difference that Malthus had identified was between two rates of growth: geometric or exponential, and arithmetic. Geometric growth is growth by compound interest, in which the increment in each period is calculated against the accumulated increases in all previous periods. If an initial amount of 100 increases by 10 percent in each period, then in each succeeding period it will be: 100, 110, 121, 133.1, 146.41, 161.051. This rate of growth leads quickly to very high values. Arithmetic growth is calculated only on the original amount, so the amount of increase is the same in each period. With an initial 100 and growth rate of 10 percent, the amount will increase as: 100, 110, 120, 130, 140, 150. Clearly the two rates diverge rapidly. Using the figures Malthus employed, with population doubling every 25 years and the population of "the Island" (Great Britain) assumed to be (in 1798) about 7 million, the results of Malthus's calculations are shown dramatically in the following table.

| GEOMETRIC AND ARITHMETIC GROWTH | | |
|---|---|---|
| **AFTER** | **POPULATION SIZE** | **SUBSISTENCE SUPPORTING** |
| 25 years | 14 million | 14 million |
| 50 years | 28 million | 21 million |
| 75 years | 56 million | 28 million |
| 100 years | 112 million | 35 million |

Clearly, such a rate of population growth cannot be sustained, and Malthus extended the argument to the population of the whole world, to demonstrate that although migration to less populous lands might relieve the pressure on resources for a time, eventually the entire planet would be overpopulated. Nor can the difficulty be resolved by assuming that food production can increase indefinitely because the divergence arises from the fact that populations increase geometrically, but food production increases only arithmetically. It is the type of growth that is the problem.

It is obvious that population growth will be checked, and in the first edition of the *Essay* Malthus asserted that the constraining factors would be accidents, famine, disease, war, and what he called "vice," by which he meant infanticide, murder, contraception, and homosexuality. Critics pointed out that this was a harsh view of humanity to be held by a clergyman. Malthus responded to this in later editions by allowing for people marrying later in life and abstaining from sex prior to and outside of marriage. He continued to maintain, however, that measures to alleviate the suffering of the poor were doomed to fail. Improving living conditions leads inevitably to an increase in population; the size of the labor force increases and wages fall while unemployment rises; and increased demand for provisions causes prices to rise. These adverse circumstances make it more difficult for people to marry and raise families, so the population tends to decrease, relieving the pressure on resources. So the cycle continues. Malthus was not a hard, unfeeling man. He was keenly aware of the injustice that allowed the rich to dwell in luxury while the poor starved, and he urged benevolence.

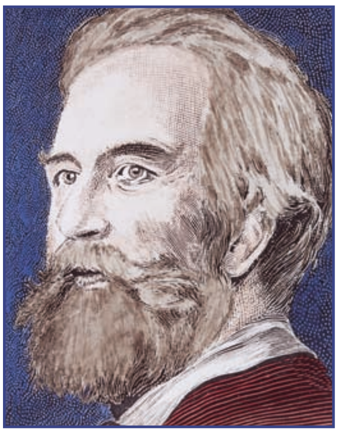
There have been many criticisms of Malthus's theory, but all of these refer to his economic and social assessment of human communities. That is not what caught the attention of Darwin and Wallace, however. They responded to the implications of the following paragraph in chapter 2 of the *Essay:*

> Among plants and animals the view of the subject is simple. They are all impelled by a powerful instinct to the increase of their species, and this instinct is interrupted by no reasoning or doubts about providing for their offspring. Wherever therefore there is liberty, the power of increase is exerted, and the superabundant effects are repressed afterwards by want of room and nourishment, which is common to animals and plants, and among animals by becoming the prey of others.

That was the key to the way natural selection operates. Malthus was concerned with populations, not individuals. He did not ask which individual offspring must perish when there was insufficient food or shelter, or an abundance of prey invited predators. That was the next step in the chain of reasoning that led to a theory of evolution by natural selection. The constraint Malthus identified arose from the relationship between plants, animals, and people and the resources available to them in their environment. Malthus had proposed an essentially ecological theory.

## ERNST HAECKEL AND "OECOLOGY," THE STUDY OF THE HOUSEHOLD

*The Origin of Species* was an immediate commercial success, but although Darwin was a gifted writer, his book had no illustrations, and many readers may have found it somewhat technical. *Natürliche Schöpfungsgeschichte* (The natural history of creation), a more popular book on evolution, appeared in 1868 in Germany, written by Ernst Haeckel (1834–1919), professor of zoology at the University of Jena. Haeckel wrote in German, but an English translation was published in 1876 with the full title *The Story of Creation: or The Development of the Earth and Its Inhabitants by the Action of Natural Causes; a Popular Exposition of the Doctrine of Evolution in General, and That of Darwin, Goethe, and Lamarck in Particular.* The illustration on page 102 shows Haeckel as he appeared at about this time.



Ernst Haeckel (1834–1919) was an enthusiastic supporter of Darwin's theory of evolution by natural selection. He coined the term *ecology.* *(Science Photo Library)*

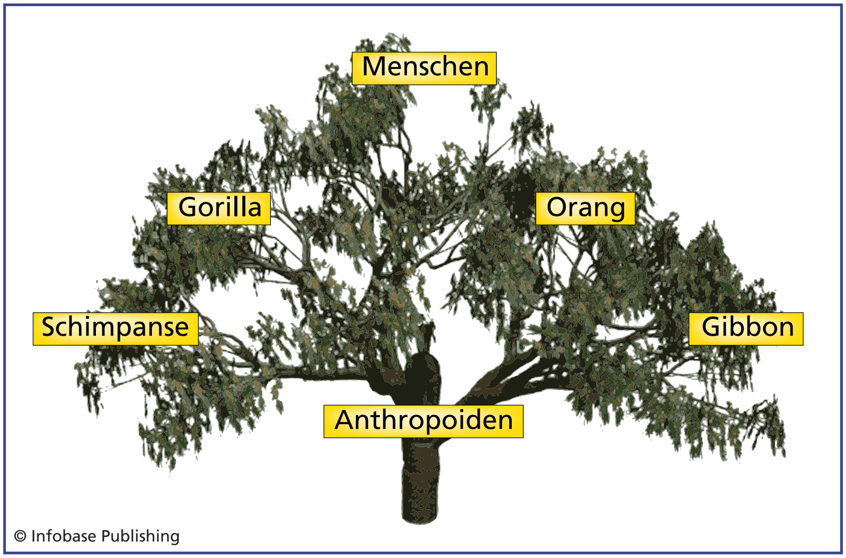
Haeckel was an enthusiastic supporter of Darwin, and his book introduced evolutionary theory to a wide audience, although the version Haeckel presented was not quite what Darwin had proposed. Haeckel believed in evolution, but he did not agree that natural selection was the only mechanism by which it occurred. He thought Lamarck was closer to the truth, with his suggestion that physical modifications organisms acquire through adapting to their environmental conditions are inherited by their offspring (*see* 'The Comte de Buffon and Geographic Isolation' on pages 74–77). Haeckel believed evolution had taken place in 22 distinct phases, the 21st phase being the "missing link" between apes and humans that he named *Pithecanthropus alalus* ("ape man without speech"). When the Dutch anatomist Eugene Dubois (1858–1940) discovered the fossil remains of "Java man" in 1891, he believed it was Haeckel's missing link and named it *Pithecanthropus alalus;* it has since been reclassified as *Homo erectus.* Haeckel was a skilled zoologist, specializing in invertebrate anatomy. He arranged living organisms in what he thought was their evolutionary order, forming a tree of life with humans at the pinnacle. The drawing shows how he presented the relationships among "anthropoids," gibbons, apes, and humans (*Schimpanse* means chimpanzees; *Menschen* means humans).

In *The Story of Creation,* Haeckel expounded ideas he had developed earlier in *Generelle Morphologie der Organismen* (General morphology of organisms), a book published in two volumes in 1866 that attracted less attention. In *Generelle Morphologie,* Haeckel explored the implications of evolution, in particular what it said about the relationship between living organisms and their surroundings. In developing this theme, he coined the word *Ökologie* to describe the study of that relationship, deriving the word from the two Greek words, *oikos* meaning house or household (the same root as the word *economy*) and *logos* meaning a discourse. It was also in 1866, during a tour lasting into 1867 that took him to the Canary Islands, that Haeckel visited England and met Darwin at his home, Down House. Mrs. Darwin later wrote to her son that Haeckel was "very nice and hearty and affectionate, but he bellowed out his bad English in such a voice that he nearly deafened us."

Haeckel also coined many other words, including *phylum, phylogeny,* and the taxonomic kingdom Protista. He named thousands of new species, and he was also an accomplished artist. His 10-volume

*Kunstformen der Natur* (Artforms of nature) contained more than 100 colored illustrations of animals, many of them marine organisms.

Scientists have abandoned many of Haeckel's ideas, particularly his theory that in the course of its development a vertebrate embryo proceeds through stages that repeat the evolutionary history of its species—an idea summarized as "*ontogeny* repeats *phylogeny*." Haeckel also maintained that the social sciences were instances of applied biology, an idea other scientists regarded as too much of a generalization (*see* 'The Rise of Sociobiology' on pages 178–185).




Ernst Haeckel believed that humans (*Menschen* in German) are the highest form of life, placing them at the top of his elaborate tree of life, a small portion of which is shown here.

Ernst Heinrich Philipp August Haeckel was born on February 16, 1834, in Potsdam, then in Prussia, the son of Carl and Charlotte Haeckel. His mother was the daughter of a privy councillor in Berlin, and his father was chief administrator for religious and educational affairs in Merseburg, in the state of Saxony-Anhalt. Haeckel began his education at the Domgymnasium (Cathedral High School) in Merseburg. After completing his studies there, in 1852 he enrolled to study medicine at the University of Berlin and later at the universities of Würzburg and Vienna before returning to Berlin, where he received his doctor of medicine degree in 1857 and a license to practice medicine a year later. Conforming to his father's wish, Haeckel began to practice as a physician in Berlin, but his interest was in anatomy rather than disease, and after a short time he closed the practice and embarked on a long trip to Italy, paid for by his father. At that time he was thinking of becoming a landscape painter, but his father disapproved, and Haeckel turned to science instead. He studied zoology at the University of Jena, obtaining a doctorate in 1860, and in 1861 he was appointed extraordinary professor of comparative anatomy and director of the university's zoological institute. In 1865 he became professor of zoology, a post that was created for him and which he held until 1909, when he retired. He was a highly talented and industrious field biologist and a prolific author. By the time he was 60, in 1894, Haeckel had written 42 books with a total of 13,000 pages, as well as many scientific papers and monographs. He was elected to many scientific academies, including the Imperial Academy of Sciences in Vienna in 1872, the American Philosophical Society in 1885, and the Royal Society of Edinburgh in 1888.

In 1862 Haeckel married his cousin Anna Sethe, who died in 1864. After her death, he married Agnes Huschke, the daughter of the German anatomist and embryologist Emil Huschke (1797–1858). They had three children. Agnes died in 1915, and from that time Haeckel became increasingly frail. He died at Jena on August 9, 1919.

## HOW "OECOLOGY" BECAME "ECOLOGY"

Ernst Haeckel defined *Ökologie* in *Generelle Morphologie* as "the comprehensive science of the relationship of the organism to the environment." In 1870 he expanded the definition to the following:

> By *Ökologie* we mean the body of knowledge concerning the economy of nature—the investigation of the total relations of the animal both to its inorganic and to its organic environment; including, above all, its friendly and inimical relations with those animals and plants which it comes directly or indirectly into contact with—in a word, *Ökologie* is the study of those complex interrelations referred to by Darwin as the conditions of the struggle for existence.

The idea inspired the Danish botanist Johannes Eugenius Bülow Warming (1841–1924; *see* "Eugenius Warming and the Ecology of Plants" on pages 136–138). Eugen Warming, the professor of botany at the Royal Institute of Technology in Copenhagen, became the first scientist to teach a university course in plant ecology, and in 1895 he published the first textbook on the subject. This was entitled *Plantesamfund: Grudtræk af den økologiske Plantegeografi.* An English translation appeared in 1909 with the title *Oecology of Plants: An Introduction to the Study of Plant Communities.*

Warming was a plant geographer, as was the German botanist Andreas Franz Wilhelm Schimper (1856–1901). Warming and Schimper combined Haeckel's approach to plant communities with the discoveries about plant distribution made by Alexander von Humboldt (*see* "Alexander von Humboldt and Aimé Bonpland, Exploring South America" on pages 79–84). Their work influenced Karl Willdenow at the Berlin Botanical Garden (*see* "Karl Willdenow and Plant Distribution" on pages 78–79), who took the opportunity of a needed overhaul of the planting scheme to rearrange the beds on ecological lines.

The English alphabet has no letters *ö* or *ø* and *oe* is commonly used, instead. That is the transliteration the translators of Warming's book used, and for a time the new science was known as "oecology," or sometimes as "oikologie," but by the time the English edition of Warming's book appeared that spelling was already falling from use. Interest in the new scientific subject spread from Europe to the United States, where botanists dropped the *o* and called their discipline "ecology."

The spelling was finally changed from "oecology" to "ecology" following a Botanical Congress held in Madison, Wisconsin, in 1893. A committee of delegates to the Madison meeting met afterward and agreed on the revised spelling—since that time "ecology" has been the standard spelling in the English language. These American botanists decided to adopt the new term to reflect their interest in the way plants adapt to their environment, in contrast to the traditional, laboratory-based study of plant physiology. The founders of the new discipline—officially the first ecologists—also hoped to broaden taxonomic studies, so plant collectors paid more attention to the environments from which their specimens were taken.

"Ecology" was not the only spelling the botanists were aiming to standardize. In 1892, at a meeting in Rochester, New York, of the Botanical Club of the American Association for the Advancement of Science, Nathaniel Lord Britton (1857–1934), the first director of the New York Botanical Garden, proposed a set of rules for the scientific naming of plants. At first it was known as the Rochester Code, and it finally became the American Code of Botanical Nomenclature. The botanists attending the 1893 Madison meeting agreed to adopt Britton's code, and it must have seemed to them an appropriate point at which to standardize the name of the new discipline.

## VLADIMIR VERNADSKY AND THE DISCOVERY OF THE BIOSPHERE

Early in 1922 the Ukrainian-Russian scientist Vladimir Ivanovich Vernadsky (1863–1945) became the first director of the Radium Institute in Petrograd (later Leningrad and now St. Petersburg). At the opening ceremony, he told his listeners that atomic power would soon be accessible, but he asked whether it would be used for beneficial purposes or for the destruction of humanity. It was the first time any scientist had warned of the dangers of nuclear energy.

Originally a soil scientist, mineralogist, crystallographer, and geochemist, Vernadsky was one of the founding fathers of geochemistry, biogeochemistry, and radiogeology, but probably his greatest contribution to science came with his work on the *biosphere*—the part of the Earth in which living organisms interact to form a steady-state system; an *ecosystem* extending over the whole planet. He described this in *Biosfera,* a book published in Russian in 1926 and translated into French as *La Biosphère* in 1929 and into German as *Biosphäre* in 1930, but not into English until 1986, and then only in an abbreviated edition. It was not until 1998 that the full English edition, *The Biosphere,* appeared. It is hardly surprising that his work is not well known in English-speaking countries, but in Russia he is regarded as one of the world's greatest scientists. His image has appeared on postage stamps, streets are named after him in Moscow and Kiev, and a train station and a Moscow subway station bear his name; libraries, museums, and one university are named after him, as are a lunar crater, a submarine volcano, a mine, the mineral vernadite, a mountain, and two ships.

Vernadsky did not coin the term *biosphere.* It was first used in 1875 by the Austrian geologist Eduard Suess (1831–1914), whom Vernadsky met in 1911, but Suess did not expand on the idea or develop the concept. The word means "the sphere of life," and Vernadsky defined its boundaries. It includes all of the world's oceans, lakes, and rivers, the atmosphere to a height of about 20 miles (32 km), and the upper part of the land surface to a depth of 1–2 miles (1.6–3.2 km)—where bacteria still manage to thrive in oil traps and subterranean moisture.

But the biosphere is much more than merely the region of the Earth in which living organisms are found. As a biogeochemist, Vernadsky studied the cycling of elements between dry land, the atmosphere, and the oceans, a process that involves living organisms, which utilize the elements as essential nutrients. He was one of the first scientists to recognize that the oxygen, nitrogen, and carbon dioxide in the atmosphere are there as a result of biological processes. This led him to the conclusion that living organisms exert a profound effect on the inanimate Earth. It was an idea that strongly influenced James Lovelock as he developed his Gaia hypothesis (*see* "James Lovelock and the Physiology of the Earth" on pages 108–112).

Vernadsky saw the emergence of the biosphere as an evolutionary process. At first the Earth was lifeless. He called this stage the geosphere. The appearance of living organisms and their colonization of the planet produced the biosphere. But the process did not end there because when human societies spread across the planet, they began to transform the biosphere. This would lead, said Vernadsky, to the development of the noosphere, also spelled noösphere, the sphere of interactive human thought; *noo-* (pronounced "no-o") is from the Greek *nous,* meaning mind. Vernadsky believed that the noosphere would emerge when scientists became able to engineer atoms, thereby altering elements, and this ability found technological applications in the production of new resources.

Vernadsky was born on March 12, 1863, in St. Petersburg. His paternal ancestors were Cossacks from the Dnieper region of Ukraine, and his father taught political economy at the University of Kiev, but his mother was Russian. Consequently, Vernadsky was both Ukrainian and Russian. In 1868 the family moved to Kharkov, where Vernadsky attended the gymnasium (high school). He graduated from the physics and mathematics department of St. Petersburg University in 1885, and from 1885 to 1890, while preparing for a higher degree, he was curator of the university's mineralogical office. He married Natalia Staritskaya in 1886, and their son, Georgy, was born in 1887 and their daughter, Nina, in 1898.

In 1890 the family moved to Moscow, and Vernadsky became professor of mineralogy and crystallography at Moscow University, a post he held until 1911, when he resigned in protest at the reactionary policies of the Tsarist government and moved to St. Petersburg. He was elected an ordinary member of the Russian Academy of Sciences in 1912. In 1918 he moved to Kiev, where he founded the Ukrainian Academy of Sciences and became its first president. He moved to Simferopol in 1919 and became rector of the Tauria University in that city in 1920.

The following year he returned to Petrograd (St. Petersburg had been renamed), where he founded the Radium Institute. Later that year he moved to Moscow. Also in 1921 Vernadsky was elected professor of mineralogy at the University of Paris (Sorbonne). He returned to Leningrad (formerly Petrograd) in 1926. From 1929 until 1945, Vernadsky headed the biogeochemical laboratory of the Academy of Sciences of the USSR, which is now the V. I. Vernadsky Institute of Geochemistry and Analytical Chemistry. He moved to Moscow in 1935.

Vernadsky traveled widely and received many honors. In 1942 he was awarded the State Prize of the USSR and the Order of the Red Banner for Labor. The Russian Academy of Sciences now awards prizes and a golden medal in his name. His wife died in 1943. Vernadsky died in Moscow on January 6, 1945.

## JAMES LOVELOCK AND THE PHYSIOLOGY OF THE EARTH

In the 1960s, when scientists and engineers were planning the *Viking* program to land instruments on the surface of Mars, James Lovelock (1919–    ), an English chemist and inventor, who was then professor of chemistry at Baylor University College of Medicine, in Houston, Texas, was a consultant to the Jet Propulsion Laboratory at the California Institute of Technology in Pasadena, California. Lovelock, who had previously helped design instruments used to analyze lunar soil, advised the NASA (National Aeronautical and Space Administration) team on instrument design. One of the biggest questions NASA hoped to answer was whether life existed on the planet. This was not Lovelock's professional concern, but the question started him thinking. If there were living organisms on Mars, they would have evolved under very different environmental conditions from those on Earth. They might use entirely different chemical reactions to metabolize food and obtain energy. Would they even be based on carbon and how would respiration work in an atmosphere containing only traces of oxygen? Almost certainly they would look totally unlike anything living on Earth. So how would scientists recognize them?

In discussions with colleagues, Lovelock came to the realization that there is one characteristic all living organisms must share, no matter how different they may be: They must absorb materials from their surroundings, process those materials to build and repair their bodies and to provide energy, and they must excrete the waste by-products of that processing. These processes should be detectable because they would alter the chemical composition of their surroundings, and the best place to look for them would be in the planet's atmosphere. This is because the mass of the atmosphere is much smaller than the mass of the solid surface or of any oceans, so if substances were being added and removed, the changes would be most easily detectable in the atmosphere. Provided chemists knew the surface gravity, surface temperature, and the energy a planet received from its star, they could calculate what gases would form an atmosphere, the chemical reactions that would take place among them, and the rate at which the reactions would proceed. From this they could predict the chemical composition of the atmosphere very precisely. If the composition of the atmosphere differed markedly from those predictions, it would indicate other, most probably biological, processes were operating.

If Lovelock was correct, it should be possible to detect the presence of life without even visiting a planet because astronomers can study the spectrum of starlight from behind a planet that passes through that planet's atmosphere. Chemical elements absorb light, each element at a different wavelength, so examining the dark lines in the light spectrum caused by absorption in the atmosphere reveals the chemical composition of the atmosphere. If that composition were not in chemical equilibrium, then scientists would have grounds to suspect the presence of life.

In the years that followed, Lovelock continued to develop this idea. He had returned from the United States and was living in Wiltshire, in southern England, earning his living as an independent scientific consultant. He enjoyed walking in the countryside, often in the company of William Golding (1911–93), the novelist and winner of the 1983 Nobel Prize in literature. As they discussed Lovelock's idea, Golding suggested that it needed a name, and proposed "Gaia." In Greek mythology, Gaia, also spelled "Gaea" and "Ge," arose from Chaos, which was the original state of the Earth, and brought forth Uranus, the sky, Ourea, the mountains, and Pontus, the sea. These figures, of Earth, sky, mountains, and sea, were Titans from whom all the Greek gods were descended, and since Gaia, the Earth, was the mother of Uranus, Ourea, and Pontus, she was also the ancestor of everything existing on Earth. It was a powerful image. Lovelock began using it, and so his Gaia hypothesis was born (*see* sidebar below).

To be useful, a scientific idea must serve two purposes. It must provide a plausible explanation for observed phenomena, and it must allow predictions to be made from it that can later be verified. To take a very simple example, gravity is a force of attraction between objects that possess mass, with a magnitude proportional to their mass and

## GAIA HYPOTHESIS

All living organisms modify their environment by utilizing materials they take from it and by discharging their metabolic waste products into it. On Earth, and on any other planet where life is abundant, these processes radically alter the planet's chemical composition. For example, Earth's atmosphere is approximately 78 percent nitrogen and 21 percent oxygen. In the world as a whole, there are about 100 lightning flashes every second. Nitrogen is chemically fairly inert, but lightning discharges release enough energy to make the gas react with oxygen ($N + O \rightarrow NO$; $NO + O_2 \rightarrow NO_3$). Nitrate ($NO_3$) is soluble in water, and eventually rain should wash all the atmospheric nitrogen to the surface. The fact that nitrogen is present in the atmosphere means that some surface process must be constantly replenishing it, and it is most likely that such a process is biological; in fact, denitrifying bacteria release nitrogen gas. Earth's atmosphere also contains both methane ($CH_4$) and hydroxyl (OH). These react in several steps to form carbon dioxide and water. Consequently, some process must be releasing methane, and at the temperatures and pressures prevailing on Earth that process can only be bacteriological. The presence of methane and nitrogen in Earth's atmosphere strongly indicates the presence of life, and there are several other examples.

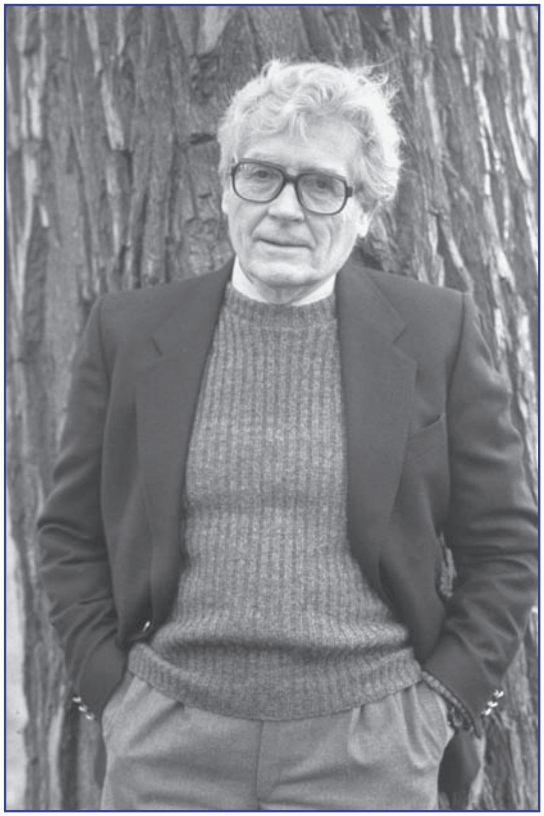
The Gaia hypothesis proposes that biological activity acts to maintain conditions favorable to life, in particular by regulating the global climate, partly through adjustments to the atmospheric content of greenhouse gases such as carbon dioxide and methane, by regulating the salinity of seawater, and by driving the cycles that return to the land essential nutrients, including iodine and sulfur, that otherwise would accumulate in the oceans. Marine organisms release dimethyl sulfide ($(CH_3)_2S$) into the air, where it is oxidized to sulfate ($SO_4$) onto which water vapor condenses to form clouds. This is the principal mechanism for cloud formation over the open oceans, and it also helps regulate the global temperature.

Biological activity on a planetary scale amounts to the management of the biosphere, such that the biosphere behaves as though it were a single organism. This does not imply intelligence or in any sense the deliberately coordinated behavior of organisms; it is simply the inevitable consequence of biological responses to prevailing conditions. In its strongest form, however, favored by some environmentalists, the Gaia hypothesis is interpreted as suggesting that in some sense Earth is a single living organism.

the distance between them. It follows, therefore, that if a small object, such as an apple, is released in the vicinity of a much more massive object, such as the Earth, the apple will move toward the Earth. Lovelock predicted that if the Earth were truly self-regulating, then any perturbation to it would trigger a biological response that could be detected, measured, and, most important, used diagnostically to characterize the perturbation that caused it.

This revealed a new dimension to the hypothesis. A recognizable biological response to a perturbation sounded very similar to a medical diagnosis of an illness, and having diagnosed an illness, a physician goes on to prescribe a treatment. It suggested that the Earth, or Gaia, might be thought of as a single organism capable of being in a state of good or poor health. Studies of the way the planet functions were therefore analogous to the physiology of a plant or animal. Lovelock called it *geophysiology,* which is the scientific study of the Earth as a total system, comprising all of its living and nonliving components.

James Lovelock (1919– ) photographed in December 1989, in a characteristic pose against a tree. Lovelock has planted many trees on land he owns in the southwest of England. *(Terry Smith/Time Life Pictures/Getty Images)*



The Gaia hypothesis has proved useful in studying certain biogeochemical cycles, but biologists remain wary of it. It is difficult to see how such a coordinated system could appear of its own accord with each feature functioning successfully as soon as it was needed. The idea has found favor with some environmentalists, however.

James Ephraim Lovelock was born on July 26, 1919, at Letchworth Garden City, Hertfordshire, to the north of London. After leaving school, he found work in a laboratory and continued studying at night school until he had the qualification needed to enroll at the University of Manchester, from where he graduated in chemistry in 1941. World War II had commenced two years earlier. Lovelock was a pacifist, strongly influenced by the Society of Friends, and as an alternative to military service he joined the staff of the National Institute for Medical Research (NIMR), which was part of the Medical Research Council. After the war, in 1946 he transferred to the Common Cold Research Unit, based in Wiltshire, where he remained until 1951. He received his Ph.D. in 1948 from the London School of Hygiene and Tropical Medicine, and in 1959 he received the degree of doctor of science in biophysics from the University of London.

In 1954, while still employed by the NIMR, Lovelock was awarded a Rockefeller Traveling Fellowship in Medicine, which he spent at Harvard University Medical School in Boston. He spent 1958 as a visiting scientist at Yale University. Lovelock resigned from the NIMR in 1961 in order to take up the professorship at Baylor University College of Medicine. In 1964 he became a freelance research scientist. The photograph on page 111 shows him as he appeared in 1989, at the age of 80.

Lovelock has received many awards. He was elected a fellow of the Royal Society in 1974. He was made a CBE (Commander of the Most Excellent Order of the British Empire) in 1990 and a Companion of Honour (CH) in 2003.

## G. F. GAUSE AND THE STRUGGLE FOR EXISTENCE

If two or more species living in the same stable environment all depend on a particular resource and use it in the same way, they will compete for access to that resource, and if the resource is in limited supply, then one of the species will be more successful than the others in obtaining it. In time, all but one of the competing species will disappear. This is known as the *competitive exclusion principle.* It happens either because one of the species competes more successfully than the others or because it is able to drive away or otherwise remove its competitors. Large size, strength, and aggressiveness are not necessarily keys to competitive success. A species that makes modest demands on the resource may fare better than a physically larger and therefore more demanding species in times of scarcity—during a spell of bad weather, for instance.

The competitive exclusion principle explains one important way that natural selection works through direct competition. The first person to describe the principle was the Italian mathematician Vito Volterra (1860–1940) in 1926, and the American mathematician Alfred J. Lotka (1880–1949) was also working on the problem at around the same time (*see* "Alfred J. Lotka, Vito Volterra, and the Mathematics of Relationships" on pages 155–158). But it was the Russian biologist and ecologist G. F. Gause who first demonstrated the principle experimentally, and although Gause fully acknowledged the prior work of Volterra and Lotka, the principle is firmly linked to Gause's name; it is often called the Gause principle or Gause's law.

In his first experiments, Gause used two species of yeasts, *Saccharomyces cerevisiae* (brewer's yeast) and *Schizosaccharomyces kephir.* Gause first grew each species separately and then grew both species together, some in test tubes with air excluded and some in flasks where the yeasts had access to air. The nutrient supply of sugar was limited, but the experiment ended before the sugar was exhausted, probably because the cells were killed by the accumulation of alcohol, which is a by-product of yeast metabolism. Gause measured the rate of growth of the two yeasts and calculated the extent to which they were competing with each other. He described this work in "Experimental studies on the struggle for existence. I. Mixed populations of two species of yeast," a paper he published in 1932 in *Journal of Experimental Biology.* Because the nutrient supply was not exhausted, Gause was observing what is now called *interference competition*—interference in which one species denies its competitor access to the resource.

For his second set of experiments, Gause used two species of *Paramecium, P. caudatum* and *P. aurelia. Paramecium* are *Protozoa*—single-celled organisms, some of which are disease-causing parasites. This time Gause grew the organisms in test tubes, adding fresh food (bacteria grown for the purpose) each day. Gause started each run of the experiment with 20 *Paramecium,* then extracted 10 percent of the test tube contents each day and estimated the numbers of each species. Once he had perfected the experimental technique, Gause found that after 16 days *P. caudatum* was no longer present. He described this work in 1934 in a book published first in Russian and then in English with the title *The Struggle for Existence.*

Although the competitive exclusion principle can be demonstrated experimentally, examples of it from field studies involve manipulating the experimental conditions. A truly natural environment is so complex that it can be very difficult to exclude all the factors that tend to mask the clear advantage one species might have over others. Nevertheless, the principle based on Gause's work soon became one of the cornerstones of ecological theory.

Georgii Frantsevitch Gause (pronounced "Gowz") was born on December 27, 1910. He was educated at Moscow University, graduating in biology in 1931, and earned his doctorate in biological sciences in 1940, working on the population structure of microorganisms growing in culture. In 1942 he and his wife, Maria Georgyevna Brazhnikova, isolated a strain of *Bacillus brevis* from which it proved possible to extract an antibiotic substance that was used to treat infected wounds. In 1946 Gause was awarded the Stalin Prize for this achievement. From 1960 until his death Gause was the director of the New Antibiotics Research Institute in Moscow, which he and his wife had founded. Gause died on May 4, 1986.

6

# The Growth of Ecology

By the final decades of the 19th century, biologists were beginning to think of plants and animals as forming communities of species. Several of the pioneers in this new field specialized in studying communities living in lakes or the sea. Aquatic species are more difficult to observe and count than those dwelling on land, but terrestrial species are free to move over wide areas, which complicates the tasks of tracking them and determining the boundaries to their living space. A lake, on the other hand, is clearly defined and contained, and its living community is quite distinct from communities on the surrounding dry land, while marine organisms are not too difficult to sample and relationships among them are relatively simple.

The initial impetus for the study of communities came from an unlikely source. Herbert Spencer (1820–1903) was a contemporary of Charles Darwin and a philosopher of evolutionary theory. He was also the person who coined the phrase *survival of the fittest.* Spencer saw that a human society resembled a single organism in which all of the citizens combined, each contributing their different work and skills, to form a unit that was more than the sum of its parts.

This chapter tells of the work of a few of these early pioneers, some of whom worked in the United States and others in Europe. Before their work could progress, however, they had to clear from their minds an ancient concept that was wholly incompatible with the idea that communities are dynamic and change over time. They had to challenge and abandon the idea of a "balance of nature."

## ABANDONING THE "BALANCE OF NATURE"

Out on the vast grassland plains of Africa, zebra and many species of antelope and gazelle graze or browse the vegetation, migrating to new pastures as the seasonal rains bring forth fresh growth. Lions, cheetahs, and other predators hunt the grazing animals. If in a particular year the rainfall is heavier than usual, plants will grow bigger and the grazers will have more to eat. Consequently, more of their offspring will survive, so their numbers will increase. More grazers mean more food for the predators, so their numbers will also increase. At some later time, a year with normal or below-normal rainfall will reduce the amount of vegetation, triggering a reduction in prey numbers, followed by a proportional drop in predator populations. Thus, as the years pass, the climate regulates the amount of plant growth, the availability of plant foods regulates the number of grazing animals, and the number of grazing animals regulates the size of predator populations. It is a simple set of relationships, and although it plays out most dramatically among the animals of the African savanna, the same relationships can be found anywhere. In the high Arctic, for instance, lemming populations fluctuate with changes in plant growth, and when lemmings are scarce, the snowy owls that prey on them move south in search of food.

The story is universal, and its underlying theme tells of balance. Through good times and bad, the proportions of vegetation, herbivores, and carnivores always remain constant when observed over long periods. Parasites, scavengers, and the soil organisms that decompose organic wastes are bound to one another in similar relationships. Naturalists have known of this, probably for thousands of years, but the concept came into greater prominence in 18th-century Europe, when naturalists began to classify plants and animals. Classification was based largely on anatomical descriptions, but it also led scientists to include information about the environment where each species was likely to be found and its relationships with other components of that environment. As they considered those relationships, many naturalists concluded that God had created each species to fulfill a particular function within an overall economy of nature. The English naturalist John Ray stressed this in *Wisdom of God Manifested in the Works of the Creation,* the book he published in 1691, and in 1713 William Derham (*see* "William Derham and the Interdependence of Organisms" on pages 52–54) expanded on Ray's work and introduced a new term, *physicotheology,* in his book *Physico-Theology; or a Demonstration of the Being and Attributes of GOD, from His Works of Creation.* Physicotheologists believed that the study of nature could reveal God's creative plan, from which it followed that natural history and theology were intimately connected. Linnaeus (*see* "Linnaeus and Binomial Nomenclature" on pages 54–67) was perhaps the most influential proponent of this view. He saw each species as occupying a place and performing a function predetermined by God at the time of the creation. If the pattern were to be perturbed, then it would automatically restore itself. This was called the "balance of nature."

The concept of a balance of nature seemed self-evident, and it strongly influenced the early conservationists, none of whom would have been troubled by the assumption underlying it: that natural communities are static. A balance clearly implies that in the long term nothing can change. If a prey population increases, then either it overexploits its food supply and is curtailed by starvation, or predation increases to reduce its numbers. In either case, the original balance is restored. This was the view of nature on which Thomas Malthus based his theory of population (*see* "Population and Resources" on pages 96–101), and it found echoes in the many warnings of the dire consequences of overexploiting natural resources, especially nonrenewable resources such as fossil fuels and minerals. The English economist William Stanley Jevons (1835–82) made one of the earliest of these predictions. In 1865 Jevons published *The Coal Question: An inquiry concerning the progress of the nation and the probable exhaustion of our coal mines,* in which he warned that eventually coal would be exhausted. He had exaggerated the rate at which coal consumption was likely to increase and, of course, he could not foresee the extent to which oil would replace coal as a primary fuel during the 20th century. The world still has plenty of coal. Malthus was also mistaken because he underestimated human ingenuity: Food production in fact kept pace with population growth, and the rate of population growth decreased as prosperity increased.

These examples illustrate the rather obvious fact that long-term predictions are usually wrong. This is especially true when the predictions are based on an assumed balance of nature. The demolition of this idea was one product of the reaction to the 1859 publication of Darwin's *Origin of Species.* Modern biologists emphasize the role of natural selection in driving the evolutionary process, but in the 19th century what many people saw in it was a depiction of a natural world where species were repeatedly challenged by rivals and by environmental changes to which they either adapted or perished. As they adapted, so species progressed. The English philosopher Herbert Spencer, one of Darwin's keenest supporters, expanded evolutionary theory into human affairs. In his nine-volume *A System of Synthetic Philosophy,* published between 1862 and 1893, Spencer argued that societies evolve through the "survival of the fittest"—a term Spencer coined and that Darwin used in later editions of *Origin.* Spencer's interpretation of Darwinian evolution came to be called *Social Darwinism.*

Within a decade of its publication, most English-speaking intellectuals had accepted the central thesis Darwin set forth in *Origin,* and they understood his evolutionary theory as implying progress. It allowed for the possibility of improvement economically and socially, and it did so by destroying utterly the idea that natural communities of plants and animals—and by extension human societies—are unchanging, that they are bound to respond to any perturbation by settling back into a preordained balance. The "balance of nature" was dead. However, it has not vanished. Even today people often refer to it, and some even go so far as to warn of the dangers of disturbing it. But scientifically and philosophically it has ceased to exist. There is no balance of nature, and with its removal ecologists were able to study the way communities change and develop over time.

## KARL MÖBIUS, HIS OYSTERS, AND THE BIOCOENOSIS

In the 1870s the Prussian ministry for agricultural affairs asked Karl Möbius (1825–1908), the professor of zoology at the University of Kiel—a German city on the coast of the Baltic Sea—to investigate the health and economic viability of the oyster beds in the Bay of Kiel. In those days the local Schleswig oysters were a famous and expensive delicacy. Some were served at the birthday banquet of Czarina Catherine II in St. Petersburg. These were natural oyster beds—the oysters were not being farmed—and gathering and exporting them was a thriving business. The authorities wished to make sure the oyster beds remained productive because demand was increasing as the expanding European railroad network opened up more distant markets. So Möbius embarked on his study of the oysters, finally reaching a conclusion regarding their future management. In his long and detailed report, published in 1877 with the title *Die Auster und die Austerwirthschaft* and in English in 1883, as *The Oyster and Oyster-Culture,* he wrote the following:

> If the oyster beds were to remain permanently productive for the general benefit of the citizens of a state as well as for the advantage of the inhabitants of the coast, then the extent of oyster fishing should not be determined by the requirements of the consumers and by the prices of oysters, but only by their annual increment of growth.

Möbius had recognized the need for sustainable management, pointing out that the harvest taken from a wild population should not exceed some proportion of the number joining the population each year. Unfortunately, but perhaps not surprisingly, his advice was ignored. Oysters were gathered faster than they could reproduce, and the Schleswig oyster business came to an end in 1925.

Karl August Möbius was born on February 7, 1825, in Eilenburg, a city in Saxony, Germany, not far from Leipzig. He began his education in the local school, and when he was 12, his father sent him to train to be a teacher. He qualified in 1844 and began work as a primary school teacher in the town of Seesen, in Lower Saxony. In 1849 he enrolled at the Humboldt University in Berlin to study natural science and philosophy. After graduating, in 1853 he taught mathematics and natural science to senior students at the Johanneum High School in Hamburg. In 1855 he married Helene Pauline Meyer; they had three children.

In 1863 Möbius opened Germany's first seawater aquarium, in Hamburg. He qualified for his doctorate in 1868 at the University of Halle, and shortly afterward he was appointed professor of zoology at the University of Kiel and director of the Zoological Museum. In 1888 he became director of the zoological collections at the Museum für Naturkunde (Natural History Museum, also known as the Humboldt Museum) in Berlin. At the same time he was appointed professor of systematic and geographical zoology at the Humboldt University. Möbius continued to work at the Humboldt University until he retired in 1905. He died in Berlin on April 26, 1908.

Möbius's 1877 report on the Bay of Kiel oyster beds was very detailed. In it Möbius described all the other invertebrate animals he found, their relationships with one another, and their relationships with the surrounding environment. His report includes the following passage (quoted from the 1883 English translation):

> Each species which lives here is represented by the greatest number of individuals which can grow to maturity subject to the conditions which surround them, for among all species the number of individuals which arrive at maturity at each breeding period is much smaller than the number of germs produced at that time. The total number of mature individuals of all the species living together in any region is the sum of the survivors of all the germs which have been produced at all past breeding or brood periods; and this sum of matured germs represents a certain quantum of life which enters into a certain number of individuals, and which, as does all life, gains permanence by means of transmission. Science possesses, as yet, no word by which such a community of living beings may be designated; no word for a community where the sum of species and individuals, being mutually limited and selected under the average external conditions of life, have, by means of transmission, continued in possession of a certain definite territory. I propose the word *biocoenosis* for such a community. Any change in any of the relative factors of a biocoenosis produces changes in other factors of the same.

In 1902 the botanists Carl Joseph Schröter (1855–1939) and Oskar von Kirchner (1851–1925) extended the biocoenosis concept in their paper *Die Vegetation des Bodensees* (The vegetation of the Bodensee); the Bodensee, also called Lake Constance, is a lake on the borders of Germany, Switzerland, and Austria. In their paper they coined the terms *synecology,* which is the overall study of complete living communities, and *autecology,* which is the study of single organisms and small populations. By the early years of the 20th century, biologists were busy defining ecological concepts, and the new science of ecology had begun to acquire its vocabulary.

## STEPHEN FORBES AND "THE LAKE AS A MICROCOSM"

On February 25, 1887, Stephen A. Forbes (1844–1930), professor of zoology and entomology at Illinois State University and state entomologist of Illinois, presented the paper "The Lake as a Microcosm" to a meeting of the Peoria Scientific Association. The paper was later published in the *Bulletin of the Scientific Association (Peoria, IL).* In 1877 Forbes had published a paper on the food of birds, and in 1878 he published another on the food of fishes. His work with fishes stimulated his deeper interest in the organisms living in freshwater lakes, and that study took him to many of the lakes in Illinois and Wisconsin as well as to Lake Michigan. Forbes had been appointed state entomologist in 1882, following the retirement of the previous incumbent, and from that time his work centered on insects, so after the 1887 paper he was able to devote less of his time to the study of life in lakes.

His paper revealed a new way of looking at plants and animals, and before commencing his detailed descriptions of lake life, Forbes introduced his approach in the following two paragraphs.

> The animals of such a body of water are, as a whole, remarkably isolated,—closely related among themselves in all their interests, but so far independent of the land about them that if every terrestrial animal were suddenly annihilated, it would doubtless be long before the general multitude of the inhabitants of the lake would feel the effects of this event in any important way. One finds in a single body of water a far more complete and independent equilibrium of organic life and activity than on any equal body of land. It is an islet of older, lower life in the midst of the higher more recent life of the surrounding region. It forms a little world within itself,—a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on so small a scale as to bring it easily within the mental grasp.
>
> Nowhere can one see more clearly illustrated what may be called the *sensibility* of such an organic complex,—expressed by the fact that whatever affects any species belonging to it, must speedily have its influence of some sort upon the whole assemblage. He will thus be made to see the impossibility of studying any form completely, out of relation to the other forms,—the necessity for taking a comprehensive survey of the whole as a condition to a satisfactory understanding of any part. If one wishes to become acquainted with the black bass, for example, he will learn but little if he limits himself to that species. He must evidently study also the species upon which it depends for its existence, and the various conditions upon which

> *these* depend. He must likewise study the species with which it comes in competition, and the entire system of conditions affecting their prosperity, and by the time he has studied all these sufficiently he will find that he has run through the whole complicated mechanism of the aquatic life of the locality, both animal and vegetable, of which his species forms but a single element.

In this paper, written 10 years after Möbius wrote about the community inhabiting the Kiel Bay oyster beds and introduced the term *biocoenosis,* Forbes was insisting that species can be understood fully only by studying them in an ecological context. At an event the University of Illinois held on March 15, 1930, to commemorate Forbes's life and work, the zoologist H. J. Van Cleave delivered an address that included the following:

> Very early in his program, he became impressed with the significance of interrelationships between organisms and their environment. Before ecology had been conceived as an offspring of the biological sciences, Professor Forbes had adopted the ecological point of view in his published writings. . . . This ecological point of view has dominated his entire program of research.

Stephen Alfred Forbes was born in a log house on a small farm at Silver Creek, in Stephenson County, Illinois, on May 29, 1844. The family were pioneers and their life was hard. Stephen was the fifth of six children. Their father died in 1854 when Stephen was 10. At that time the family was living in a one-room house on a heavily mortgaged 140-acre (57-ha) farm. Henry, the eldest son, was 21 and had left home, but he returned and assumed responsibility for raising the family. Henry taught Stephen from 1858–1860, preparing him to enter Beloit Academy, where he spent one year before enlisting in the army in 1861. Forbes fought in the Civil War, being captured by Confederate forces in 1862 and spending four months as a prisoner of war. He left the army in 1865, and in 1866–67 he studied medicine at Rush Medical College. In 1867 he spent some time growing strawberries before resuming his medical studies at Makanda, Illinois. From 1868 to 1872 he taught in schools in several Illinois towns while studying science in his free time. In 1872 he became curator at the Illinois State Natural History Museum, remaining in the post until

1877, when he founded and was director of the Illinois State Laboratory of Natural History. He held this position until 1917. From 1875 to 1878 he was also an instructor in zoology at the Illinois State Normal University. Forbes received his Ph.D. from Indiana University in 1884. He was Illinois state entomologist 1882–1917, professor of zoology and entomology at the University of Illinois 1884–1909, professor of entomology from 1909 until his retirement, and dean of the College of Science at Illinois University 1888–1905. In 1912 he was elected president of the Entomological Society of America and the Ecological Society of America. He was made chief of the Illinois State Natural History Survey in 1917, and in 1918 he was elected to the National Academy of Sciences. He retired as emeritus professor in 1921. Forbes died at Urbana, Illinois, on March 13, 1930.

## FRANÇOIS-ALPHONSE FOREL AND THE INHABITANTS OF LAC LÉMAN

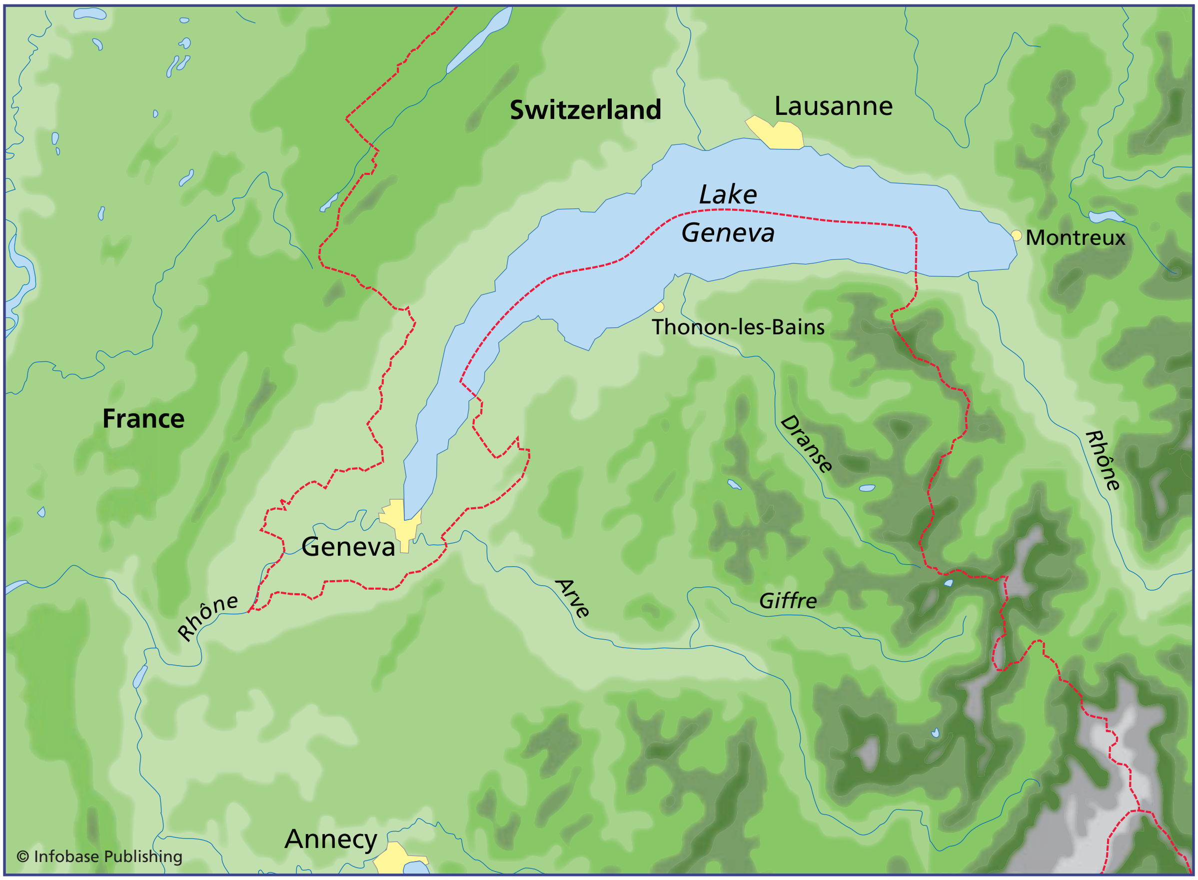
At the University of Geneva, Switzerland, there is an Institut F.-A. Forel, which is dedicated to the study of lakes and rivers. It is named after François-Alphonse Forel (1841–1912), the Swiss scientist who founded that study and who called it *limnology,* which is the name it still bears. The honor is appropriate because Geneva lies on the shore of the second-largest lake in central Europe, and the city prides itself on its beautiful situation. The map on page 124 shows the lake's location on the border between Switzerland and France, with Geneva in the western corner and the city of Lausanne near the other end. The crescent-shaped lake is called Lake Geneva, especially around the city of Geneva, and the French know it as Lac Léman, from Lacus Lemannus, which was the name the Romans gave it.

Between 1892 and 1904, F.-A. Forel published a three-volume work, *Le Léman: Monographie limnologique* (Léman: limnological monograph), describing the lake and the communities of organisms living in it. In the following words from the first chapter, Forel explained how he came to coin the word *limnology.*

> The subject of this book is dealing with a part of the Earth and, therefore, is geography. The geography of the oceans is in turn called *oceanography.* But a lake, as big as it may be, is by no means an ocean. Its limited area gives it a special feature which is very

> different from the endless ocean. I had to find a more modest word to describe my investigations, such as the word *limnography.* But, because a limnograph is a device to measure the water level of lakes, I had to coin the new word limnology. *Limnology* is in fact the *oceanography of lakes.*

Lac Léman is big. It is 45 miles (73 km) long, up to 8.7 miles (14 km) wide, and it has a surface area of 225 square miles (582 $km^2$). In places it is 1,017 feet (310 m) deep. Only Lake Balaton in Hungary is larger, by about 4 square miles (10 $km^2$). Winds blowing across a large lake, or any other partly enclosed body of water, alter the air pressure




Lake Geneva, also called Lac Léman, is the second-largest lake in central Europe. The line through its center is the border between Switzerland to the north and east and France to the west and south. The Swiss cities of Geneva and Lausanne are located on its shores.

over the water surface and this can sometimes make the water oscillate rhythmically up and down. The oscillation produces standing or stationary waves called *seiches.* These often last for only a few minutes, but they can remain in place for up to two days. Forel was the first scientist to study them as part of his Lac Léman research.

Lakes in the European Alps, including Lac Léman, receive water from glaciers. Glacial meltwater is very cold, and it sinks directly to the bottom of the lake because its temperature means it is denser than the surface water, which is warmed by the Sun. The cold, dense water flows across the bottom of the lake, forming *density currents*—currents produced by differences in density between adjacent bodies of water. Forel discovered density currents and was the first scientist to study them. He described seiches and density currents in the standard work on limnology, *Handbuch der Seenkunde* (Handbook of lake science), which he published in 1901.

Forel also studied earthquakes, and in 1881 he published a scale of earthquake intensities. The Italian geologist and volcanologist Michele Stefano de Rossi (1834–98) had already published a scale in 1874. The two then collaborated in producing a 10-point scale in 1883. For many years the Rossi–Forel scale was the most widely used earthquake intensity scale, and it was the first to be used internationally. In 1902 the Italian volcanologist Giuseppe Mercalli (1815–1914) devised a 12-point scale that replaced it.

François-Alphonse Forel was born at Morges, Switzerland, on February 2, 1841. Morges is not far from the small town of St. Saphorin, on the northern side of Lac Léman in the canton of Vaud. As the illustration on page 126 shows, it is a spectacularly beautiful place, and from a very young age Forel's father encouraged him to take an interest in the lake. Forel studied at the Collège de Genève (Geneva College) from 1857 to 1859, then studied medicine at the University of Montpellier, France, and later in Paris and at the University of Würzburg, Germany, where he qualified in 1867. Forel then became a professor at Würzburg. He moved back to Switzerland as professor of anatomy and general physiology at the Académie de Lausanne (Lausanne Academy) from 1871 to 1875 and then professor of comparative anatomy. He resigned from the academy in 1895 in order to devote himself exclusively to research. Forel contributed to his community, serving as a councillor in Morges (1867–1909) and as a deputy in the Grand Council of the Vaud canton (1870–74). Forel died at Morges on August 7, 1912.

Set in the heart of central Europe, Lake Geneva (Lac Léman) is famous for its spectacular scenery. This is a view looking south from St. Saphorin, near Morges in the Swiss canton of Vaud. *(Stone/Getty Images)*

## VICTOR HENSEN, KARL BRANDT, AND STUDIES OF SEA LIFE

When biologists began to study the distribution of marine life, it seemed natural to suppose that warm waters were more hospitable than cold waters. After all, Antarctica has no native land mammals because the climate is too cold and there is no food for them. There are land mammals living in the Arctic, but there are far fewer native Arctic species than there are species native to warmer climes farther south. That is what biologists believed, but no one had actually checked whether it was true. The first person to do so was the German zoologist Victor Hensen (1835–1924). Between 1871 and 1891, while he was professor of physiology at the University of Kiel, Hensen led several expeditions to Greenland, the Baltic and North Seas, and to the tropical regions of the Atlantic Ocean. To everyone's surprise, Hensen found that life was more abundant in cold waters than in warm waters. Ernst Haeckel (*see* "Ernst Haeckel and "Oecology," the Study of the Household" on pages 101–104) rejected his findings, saying that Hensen's sampling techniques were faulty, but other scientists checked them, found them to be correct, and little by little biologists were forced to accept that Hensen had been right, and that cold seawater is much richer in life than warm seawater.

Hensen invented devices for collecting samples of very small marine organisms. The illustration on page 128 shows one of these, which he invented in about 1883 and that he called a *Korbnetz* (basket net). It comprised a metal cone containing a conical net. When it was lowered through the water, small organisms became ensnared in the mesh of the net, from which they could be extracted for study.

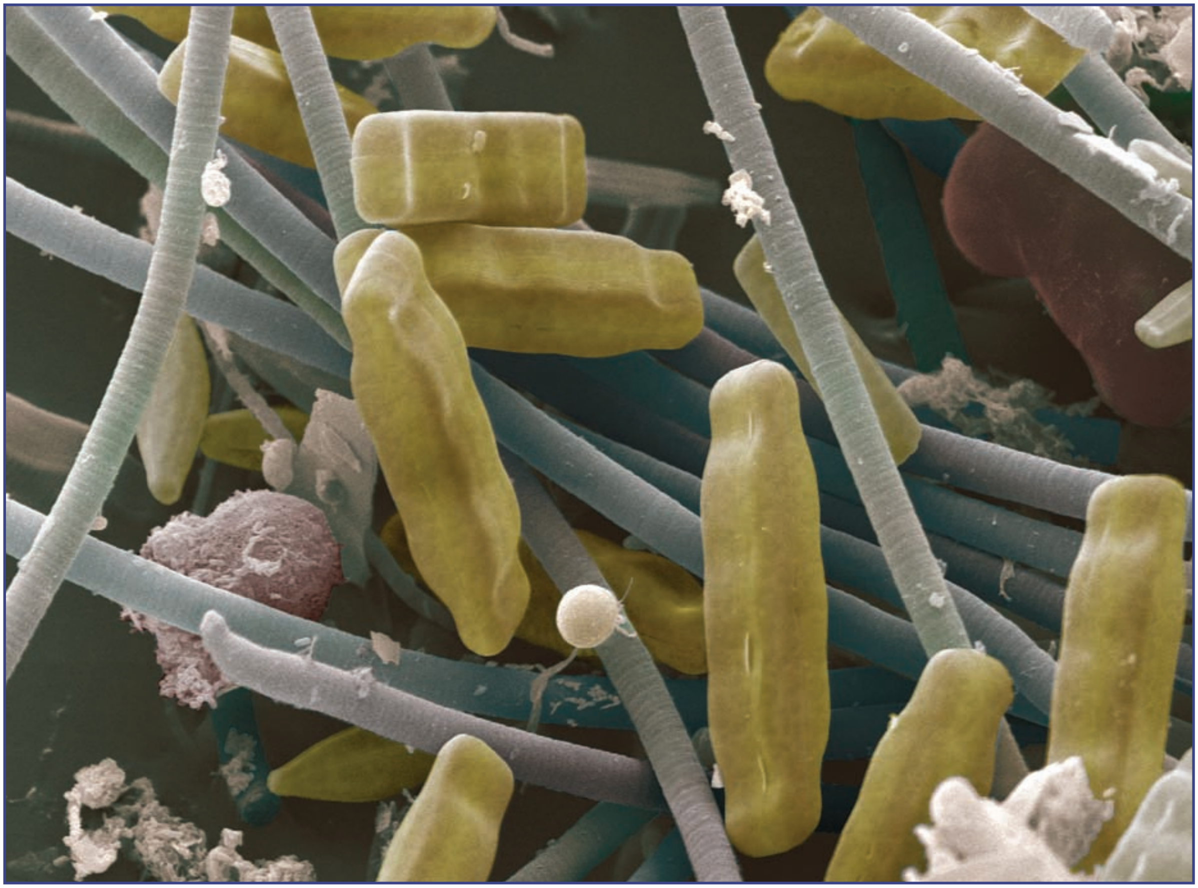
When he examined the contents of his fine-meshed nets under a microscope, Hensen discovered a bewildering variety of tiny organisms. They included single-celled *algae*—simple plantlike organisms, lacking stems, leaves, or roots, which perform photosynthesis. There were *diatoms*—algae enclosed in elaborately patterned cell walls containing silica. These cell walls, called *frustules,* were in two halves that overlapped. He found bacteria forming long strands. These were *cyanobacteria*—bacteria that perform photosynthesis. The photograph on page 129 taken with a scanning electron microscope, shows diatoms and strands of cyanobacteria enlarged 610 times.

Hensen also found the eggs and larvae of larger marine animals, the larvae feeding on the algae or preying on one another. These microscopic organisms constituted a complex community. They were far too small to be able to swim against the currents, so they drifted with the surface waters. Scientists already knew that the surface waters of the oceans contained what they called "floating stuff" (*Auftrieb* in German). Where the water is biologically rich, these organisms color the sea green; clear water indicates an absence of marine life. Hensen found *Auftrieb* an inadequate name, and (translated into English) he wrote the following:

> However, the expression “Auftrieb” does not describe the floating matter sufficiently. I prefer to call this material “Halyplankton.” Since this contribution is only concerned with the oceans I will use the shorter expression “plankton.” I define plankton as everything that drifts in the water, whether in the upper or deeper layers, and whether dead or alive.
>
> In general, I assume, plankton can grow anywhere in the oceans. It consists of living nutrition for others, and it seems to be an excellent source of nutrients.

Hensen had coined the word *plankton,* deriving it from the Greek *plagktos,* which means “wandering.” Christian Andreas Victor Hensen was born on February 10, 1835, in the city of Schleswig, in northern Germany. He studied medicine at the universities of Würzburg, Berlin, and Kiel, qualifying at Kiel in 1859. Hensen became a member of the Prussian House of Representatives in 1867 and used his position there to promote plans for ocean research. He was instrumental in establishing the Royal Prussian Commission for the Exploration of the Oceans. Hensen was professor of physiology at Kiel from 1871 to 1891, and his research covered human embryology and anatomy as well as marine biology. While at Kiel, with the help of a government subsidy to investigate fish stocks, Hensen assembled a team


One of a number of devices Victor Hensen (1835–1924) invented for sampling marine plankton; he called this the *Korbnetz* (basket net). It was lowered through the water, trapping organisms in a conical net on the inside. Hensen invented it in about 1883.



An image of marine plankton, magnified 610 times, captured by a scanning electron microscope. The blue strands are colonies of single-celled cyanobacteria (formerly called blue-green algae). The yellow bodies are diatoms, which are single-celled algae, each with an intricately patterned cell wall or frustule. *(Andrew Syred/Science Photo Library)*

of biologists which became known as the Kiel school. He died on April 5, 1924.

Karl Brandt (1854–1931), a protégé of Hensen, took Hensen's study of plankton a stage further. In 1883 Brandt published a treatise with the title *On the morphological and physiological importance of chlorophylls in animals,* in which he coined the word *zooxanthella,* from the Greek words *zoo* (animal), *xanth* (yellow), and *ella* (diminutive), so according to his original definition zooxanthellae are microscopic yellow animal cells. Brandt found them living inside the cells of radiolarians—single-celled protozoons with silica cell walls. In fact the zooxanthellae Brandt saw are also protozoons, but much smaller than the cells they inhabit.

Brandt thought the organisms he identified might be living mutualistically: *Mutualism* is an intimate relationship between two species that benefits both. Hensen had studied the geographic distribution of plankton, but Brandt concentrated more on the seasonal changes in planktonic populations in the northern oceans, where the climate is strongly seasonal. He found that the chemical nutrients available to the plankton varied over the annual cycle and that the increase in nutrient supply combined with rising temperature and intensity of sunlight caused a springtime bloom of marine algae. The German biologist Alexander Nathansohn (1878–1940) later modified Brandt's discovery by pointing out the importance of vertical movements of the seawater in bringing nutrients from the seafloor to the surface waters.

Brandt's work, building on that of Hensen, stimulated the study of microscopic marine life and especially the study of corals. Biologists had been observing and studying marine organisms since the beginning of microscopy in the 17th century, but members of the Kiel school concentrated not on individual species, but on relationships among populations of species that formed communities, such as the plankton. Their work led to the establishment of the Marine Biological Association in Plymouth, England, with a laboratory that opened in 1888, and in 1930 of the Woods Hole Oceanographic Institution in Massachusetts. These are two of the world's major marine laboratories of the present day.

7

# Social Organization of Plants

Herbivorous animals feed on plants. Carnivores hunt the herbivores. Ecological relationships are to a large degree those of the hunter and the hunted. The English poet Alfred, Lord Tennyson (1809–92) wrote the following famous lines as Canto 56 of his long poem *In Memoriam A.H.H.* mourning the death of his friend Arthur Henry Hallam at the age of 22:

> Who trusted God was love indeed
> And love Creation's final law—
> Tho' Nature, red in tooth and claw
> With ravine, shriek'd against his creed—

Tennyson completed *In Memoriam* in 1849, seven years before the publication of *The Origin of Species,* and his poem was published anonymously the following year, but the idea of evolution was in the air, and that idea implied that natural events routinely occurred without divine intervention. Many, including Tennyson, found this troubling. In these lines he confronted the traditional belief of a universal divine love with the reality of biological relationships and the natural event that had robbed him of his friend. The poet did not coin the phrase "tooth and claw"; he merely used an expression that was already commonplace.

Dogs, cats, eagles, sharks, crocodiles, snakes, and other predators kill the animals on which they feed, using teeth, claws, venom, and such other weapons as they may possess. The killing often appears cruel, and it is often bloody. But it is far from being the whole ecological story.

Plants also have relationships with one another. During the 19th century, botanical geographers had plotted the distribution of plant families over large areas of the world, and they noted that particular types of plants commonly occurred together. The plants formed communities, and botanists began to study those communities. This chapter outlines the development of that branch of ecology, which led to the establishment of yet another scientific discipline: *phytosociology,* which is the classification of plant communities according to the characteristics and relationships of and among the plants within them.

## OSCAR DRUDE AND PLANT COMMUNITIES

A map in an atlas may depict a large area as covered by a particular type of natural vegetation—such as boreal (northern) forest, tropical forest, or desert—and this is likely to be perfectly accurate, so far as it goes. A visitor to such an area will find wide local differences, however. Even a desert is not a wholly arid wilderness of sand dunes or bare rock; there are oases where plant life is luxuriant. In the boreal forest that forms a belt dominated by coniferous trees such as pine, fir, and spruce across the northern part of North America and Eurasia, the hilltops are often bare, and conifers are not the predominant plants growing in sheltered river valleys and around some lake shores. In 1896 Oscar Drude (1852–1933), the director of the Dresden Botanical Gardens, published *Die Ökologie der Pflanzen* (The ecology of plants). In this book Drude showed how local factors—hills, valleys, local variations in temperature and precipitation—influenced the composition of plant communities. It was the book that made Drude one of the founders of the science of plant ecology.

Oscar Drude was born in Brunswick, Germany, on June 5, 1852. In 1870 he enrolled at the Collegium Carolinum (now the Technical University) in Brunswick to study natural science and chemistry, and in 1871 he advanced from there to the University of Göttingen, where he became an assistant to the distinguished German botanist August (Heinrich Rudolf) Grisebach (1814–79). Drude received his Ph.D. at Göttingen in 1873 and became an assistant to the plant collector Friedrich Gottlieb Theophil Bartling (1798–1875), who was in charge of the university's herbarium. From 1876 until 1879, Drude was a lecturer at the university.

In 1879 Drude moved to Dresden to take up an appointment as professor of botany at the polytechnic. In 1890 the polytechnic became a new technical high school, and Drude was in a strong position to influence the organization of scientific research and teaching. Also in 1890 Drude became director of the Dresden Botanical Gardens. He twice served as rector of Dresden Technical High School (1906–07 and 1918–19), and in 1920 he was made professor emeritus of botany. Drude died at Bühlau, near Dresden, on February 1, 1933.

Drude wrote and coauthored several important works. The first was his *Atlas der Pflanzenverbreitung* (Atlas of plant distribution) in 1887. *Handbuch der Pflanzengeographie* (Handbook of plant geography) appeared in 1890. He coedited with Adolf Engler (1844–1930) *Die Vegetation der Erde* (The vegetation of the Earth), which appeared between 1896 and 1928.

The first scientist to define and use the phrase *tropical rain forest* was another German botanist and plant geographer, Andreas Franz Wilhelm Schimper (1856–1901), in *Pflanzengeographie auf Physiologischer Grundlage* published in 1898; the first English language edition appeared in 1903, with the title *Plant Geography on a Physiological Basis.* It was in this work that Schimper described what he called *tropische Regenwald* (tropical rain forest) as being "evergreen, hygrophilous in character, at least thirty meters high, rich in thick-stemmed lianes, and in woody as well as herbaceous epiphytes." It is the definition that remains in use today. *Lianes* or lianas, are free-hanging climbing plants; *epiphytes* are plants that grow on the surface of other plants, using their hosts only for support so they are not parasites.

Schimper also observed that in Europe, with its temperate climate and almost all of its lowland areas farmed, local changes in natural plant communities were not very evident. Plant geography, leading to phytosociology, began to develop only when European botanists began to travel the world, experiencing firsthand the plants of the humid Tropics, tropical deserts, and tundra.

## JOSIAS BRAUN-BLANQUET AND PHYTOSOCIOLOGY

August Grisebach (1814–79) was one of the most influential botanists in Europe. He was a taxonomist who devised a way of identifying and naming large units of vegetation, and he described this in his book *Die Vegetation der Erde nach Ihrer Klimatischen Anordnung* (The vegetation of the Earth after its climatic arrangement), published in two volumes in 1872. Grisebach's work led to the concept of the *floral province,* which is a geographically large area supporting a distinctive type of vegetation with many *endemic* species—species found nowhere else.

Grisebach set the pattern for the approach European plant ecologists adopted to the study of plant communities. The scientist who developed it most fully, producing a complete classification scheme, was the Swiss plant ecologist Josias Braun-Blanquet (1884–1980). During his long life, Braun-Blanquet came to dominate European phytosociology through the team of scientists he assembled around him. This became known as the Zurich School of Phytosociology, and from 1930, when the team moved to Montpellier, France, it was known as the Zurich–Montpellier School of Phytosociology (*see* sidebar on page 135). The location moved because Braun-Blanquet had been appointed director of the newly established International Station for Alpine and Mediterranean Botany, at Montpellier. The institution's French name is Station Internationale de Géobotanique Méditerranéenne et Alpine. This long name is usually abbreviated to SIGMA, and the Zurich–Montpellier approach to phytosociology—which continues to thrive—is sometimes known as Sigmatism.

At the time when Braun-Blanquet developed his method, plant ecologists were dividing into two groups. One group concentrated their studies on the physiology of plants, the other on classification. Braun-Blanquet favored the classification approach, and he sought to extend traditional botanical classification to cover entire communities of plants. He had little time for botanists who were not trained in taxonomy and could not reliably identify the plants they found in their field surveys. The Zurich–Montpellier, or Sigmatist approach was academic in the sense that it dealt with the classification of plant communities without any need to relate that classification to practical needs such as agriculture or conservation. It was the approach that came to dominate plant ecology throughout Europe, except for the United Kingdom, where ecologists worked along lines similar to those followed in the United States (*see* "American Ecology" on pages 139–164 and "British Ecology" on pages 165–177).

## THE ZURICH–MONTPELLIER SCHOOL

In 1928 the Swiss ecologist Josias Braun-Blanquet (1884–1980) published a book entitled *Pflanzensoziologie* (Plant sociology), based on his studies of the plant species he had found on Mount Aigoual, in the Cévennes region of France. The book proved highly influential, and he revised it for its third edition in 1964. In his book Braun-Blanquet had set out a method for classifying plant communities. Braun-Blanquet and his colleagues began developing and applying this scheme at the University of Zurich, Switzerland, and they became known as the Zurich School of Phytosociology. In 1930 Braun-Blanquet became director of the Station Internationale de Géobotanique Méditerranéenne et Alpine, at Montpellier, in the south of France, and from that time they were called the Zurich–Montpellier School of Phytosociology.

The Zurich–Montpellier method begins by surveying an area to identify the species that is most characteristic of the vegetation within it. The characteristic species indicates the type of environment, and that species together with the other plants in the area constitute a *relevé*. Relevés are then ranked hierarchically according to their geographical extent, with a phytosociological class occupying the largest area. The ranks in the hierarchy are identified by adding a specified ending to the stem of the name of the characteristic genus. The ranks and endings are as follows:

| RANK | ENDING |
|---|---|
| Class | -etea |
| Order | -etalia |
| Alliance | -ion |
| Association | -etum |
| Subassociation | -etosum |
| Variant | species name, with no special ending |

Josias Braun-Blanquet was born as Josias Braun at Chur, Switzerland, on August 3, 1884. He trained to be a shopkeeper while studying the plants around his home in his free time. The experience he gained observing the local flora allowed him to find employment from 1905 to 1912 as an assistant to the Swiss plant ecologists Heinrich Brockmann-Jerosch, Eduard Rübel, and Carl Schröter. From 1913 to 1915, he studied at the University of Montpellier under the French botanist Charles Flahault (1852–1935). Braun began his own research while still a student. The Swiss National Park was established in 1914, and between 1914 and 1921 Braun set up approximately 30 permanent experimental plots in the park, where the development of plant communities could be monitored over a long period (in 1939 the ecologist Balthazar Stüssi increased the number to 160). In 1915 Braun received his Ph.D. from the University of Montpellier. The same year he married a fellow student, Gabriella Blanquet. Following his graduation, Braun-Blanquet, as he then was, became an assistant to Rübel until 1922, when he obtained the post of lecturer at the Cantonal Technical High School in Zurich. He remained at Zurich until 1926, during which time he formed the Zurich School. In 1926 he returned to live in Montpellier, earning his living as a private teacher. He was appointed the first director of SIGMA in 1930 and remained in that position until his death. Braun-Blanquet died at Montpellier on September 20, 1980.

The Zurich–Montpellier School had two European rivals, based in Sweden and Estonia. The Estonian school was established in 1934 by Professor Teodor Lippmaa (1892–1943) at the University of Tartu, and its first task was to map the plant distribution throughout the country. This was completed in 1955. The plant communities were then grouped into associations on the basis of soil type, and the associations were grouped according to the predominant plant species and the amount of water available to them, so the grouping proceeded from the most arid to the wettest environments.

The Swedish school was founded by Gustaf Einar du Rietz (1895–1967) in 1921. Du Rietz became professor of botany at the University of Uppsala in 1934, and this school is known as the Uppsala School of Phytosociology. At first it developed independently of the Zurich–Montpellier School, but in time the two schools merged many of their ideas. Today they differ only in the emphasis they place on different aspects of their classifications.

## EUGENIUS WARMING AND THE ECOLOGY OF PLANTS

Eugenius Warming (1841–1924), professor of botany at the Royal Institute of Technology in Copenhagen, was the first scientist to teach a university course in plant ecology and the first to publish a textbook on the subject (*see* “How ‘Oecology’ Became ‘Ecology’” on pages 104–106). Warming had been inspired by Ernst Haeckel’s description of the study of organisms as communities, the study for which Haeckel had coined the term *oecology.* Warming was an excellent and popular teacher, and despite the fact that he wrote in Danish, a language few foreign scientists could read, his ideas were hugely influential, especially in the English-speaking world. Once his 1895 textbook, *Plantesamfund: Grundtræk af den økologiske*

*Plantegeografi* had been translated into other languages, teachers elsewhere began to make use of it. The first English translation, *Oecology of Plants: An introduction to the study of plant-communities,* appeared in 1909, published by the Clarendon Press, Oxford. Warming's book was translated into German in 1896 and again in 1902, into Polish in 1900, and into Russian in 1901 and again in 1903. It was this book, which he read in a German edition, that persuaded Arthur G. Tansley to become an ecologist (*see* "Arthur G. Tansley, Exploring British Plants" on pages 166–170), and the American ecologist Henry Chandler Cowles (*see* "Henry Chandler Cowles and the Sand Dunes of Lake Michigan" on pages 142–145) was also strongly influenced by it.

Warming based *Plantesamfund* on lectures he had given at the University of Copenhagen. These, and his book, provide an introduction to all of the world's major *biomes*—the largest biological units recognized, covering large areas and coinciding approximately with climatic regions. It was not simply a book about plant geography, however. Warming explained how biological communities tended to solve particular environmental problems in similar ways, so that similar environments usually produced similar communities. These communities might consist of entirely different and only distantly related species, but they survived despite their differences because they had adapted to the conditions in which they lived. Cacti, for instance, are adapted to arid conditions, and they occur naturally only in the Americas. Their Old World equivalent, found in African deserts, are euphorbias, some of which are so similar to cacti that the two can be difficult to tell apart. Sidewinding, a method of locomotion that allows a snake to move across loose sand, is often associated with the American sidewinder (*Crotalus cerastes*), which is a species of rattlesnake. But sidewinding is also employed by at least three species of snakes that inhabit Old World deserts. There are countless other examples to reinforce Warming's point that adaptation to local conditions led to physiological changes, with the result that similar physical and chemical pressures produced unrelated plants and animals of similar appearance and behavior. Although he was a strong believer in adaptation, however, Warming never accepted Darwin's theory of evolution by natural selection. Warming believed that characteristics organisms acquired during their lifetime through adaptation to local conditions could be inherited by their offspring, and it was in this way that evolution proceeded. Biologists no longer accept this view.

Johannes Eugenius Bülow Warming was born on November 3, 1841, on the Danish island of Mandø, where his father, Jens Warming (1797–1844), was the minister. His mother was Anna Marie von Bülow af Plüskow (1801–63). Following his father's death, Warming and his mother moved to Vejle, in Jutland. Warming attended high school in the town of Ribe, and in 1859 he began to study natural history at the University of Copenhagen. He interrupted his studies from 1863 to 1866 to work as a secretary to the Danish paleontologist Peter Wilhelm Lund (1801–80) in the tropical grasslands of Brazil. Warming obtained his doctorate from the University of Copenhagen in 1871. He was a lecturer in botany at the university from 1873 to 1882, when he was appointed professor of botany at the Royal Institution, Stockholm, Sweden. He held this post until 1885. From 1886 to 1911, Warming held the position of professor of botany and director of the botanical gardens at the University of Copenhagen, but he was absent from Denmark from 1890 to 1892, engaged in fieldwork in Venezuela and the West Indies; in earlier years fieldwork took him to Greenland, Norway, and the Faroe Islands. He was rector of the university from 1907 to 1908. Warming received many honors. He was a member of the Royal Danish Academy of Sciences and Letters from 1878 and an honorary fellow of the Royal Society of London.

After his retirement, Warming was succeeded in his post at Copenhagen University by another influential plant ecologist, Christen Christensen Raunkiaer (1876–1960). He developed a system for classifying plants by the position of their *perennating buds*—the buds from which growth resumes after the plant has died down during the winter—in relation to the soil surface.

Warming married Johanne Margrethe Jespersen (1850–1922) in 1871. They had eight children. Eugenius Warming died in Copenhagen on April 2, 1924.

8

# American Ecology

While most plant ecologists in mainland Europe concentrated on classifying communities, American ecologists picked up another strand of Eugenius Warming's work. Warming had pointed out that each year plants release vast quantities of seeds or spores that travel unpredictably into new areas. They may fall in an environment they find hospitable or onto poor soil or among more vigorous competitors. A few survive and grow into new plants, but the great majority perish. It follows, therefore, that if all the plants were to be cleared from an area of land, the vegetation that grew up to replace it might well differ from the original, simply because of the chance arrival of seeds and spores. Americans turned their attention to the ways in which plant communities can change.

This chapter outlines the development of ecological research and ideas in North America. American scientists transformed ecology into a much more rigorous discipline than it had been previously. They were less interested in listing and describing the species that were present—important and necessary though this is—than in predicting what happens when communities are disturbed. Ecology became much more mathematical.

Many scientists have contributed to the advance of American ecological studies, and it is impossible to acknowledge all of them. But all ecologists would agree that certain figures stand out for their insight and the new research directions they pioneered. The chapter tells of those scientists and their work.

## CHARLES C. ADAMS AND THE SURVEY OF ISLE ROYALE

Isle Royale is an island 206.73 square miles (535.43 $km^2$) in extent, located in Lake Superior, Michigan, close to the Canadian border. In the 1930s the island became the center of a national park comprising about 200 islands, and today there are no permanent human residents, although there are limited facilities for visitors. The island is covered mainly by boreal forest, similar to the landscape surrounding Lake Superior, in Ontario and Michigan. The photograph below of moose attracted to a natural salt lick on the shore of Hidden Lake shows a typical landscape. Hidden Lake is one of several freshwater lakes on the island. There were no moose on the island until the early years of the 20th century, when a few swam across from Minnesota. Their descendants thrived until an unusually harsh winter in 1949, when a pair of wolves crossed to the island by an ice bridge from Ontario.

In 1905 the University of Michigan prepared a report under the direction of Charles C. Adams with the title *An Ecological Survey in*

Two moose are drawn to the shore of Hidden Lake, on Isle Royale, Michigan, by a natural salt lick. *(National Geographic)*

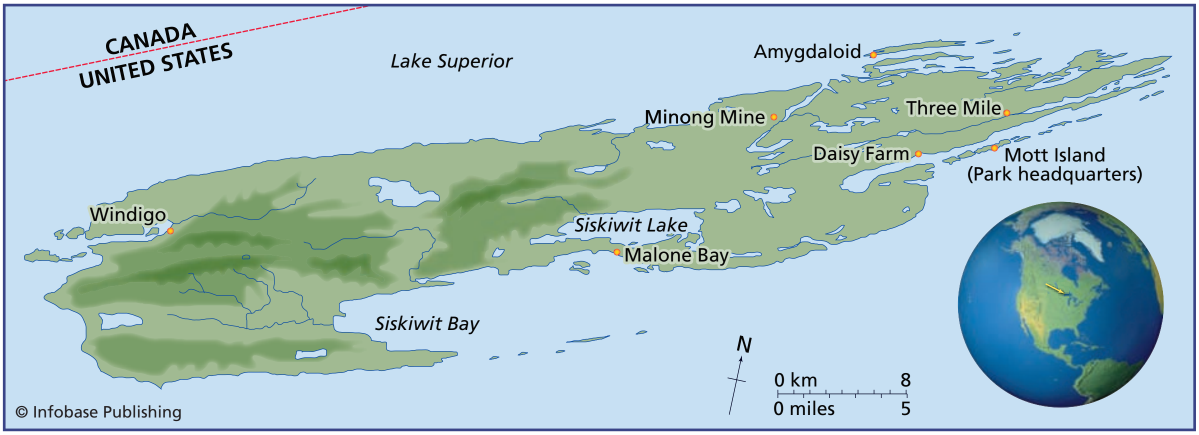
*Northern Michigan.* The State Board of Geological Survey published the report the following year as part of its own annual report and as a contribution to a wider biological survey of the State of Michigan. The accompanying letter of transmittal, signed by Alfred C. Lane, described the report as "the result of a natural history survey made in the Porcupine Mountains and on Isle Royale by a party from the University Museum, University of Michigan," and went on to explain that:

> It is not a mere list of plants and animals, but a study of those forms in relation to their surroundings. It is thus a contribution to the natural history of the Upper Peninsula, and in addition to its scientific value will, I trust, be of use to teachers in all parts of this region and stimulate them in the study of the forms of life about them.

Alfred Charles Lane (1863–1948) was a geologist, and at the time of this report he was state geologist for Michigan. The report, however, and the study it described, were the work of Charles C. Adams (1873–1955), and it was possibly the earliest ecological survey to be carried out in North America. The map on page 142 shows the island he studied. Adams was a pioneering ecologist in more senses than one: In 1908, at the University of Chicago, he became the first American to be awarded a Ph.D. in ecology, rather than qualifying as a zoologist or botanist and specializing in ecology later. He undertook the Isle Royale and Porcupine Mountains study while working at the University of Michigan Museum. Adams also worked at the University of Cincinnati Museum, and he believed that museums had an important part to play in linking field research and education.

Adams was an animal ecologist with a particular interest in predators. In the early decades of the 20th century, many biologists thought that predatory mammals such as wolves, coyotes, and mountain lions were a danger to people and harmful to other wildlife, and that their populations should be reduced. Adams disagreed, and in 1924 he proposed a plan for the conservation of North American mammalian predators on public lands, with a list of reasons for preventing their disappearance. His principal reason was their ecological importance as controls on populations of herbivores.

Charles Christopher Adams was born in Clinton, Illinois, on July 23, 1873. He graduated in 1895 from the Illinois Wesleyan




Isle Royale, Lake Superior

University and worked there for a year as an assistant biologist before moving to the Illinois State Laboratory of Natural History as an assistant entomologist, where he worked from 1896 to 1898. He received his master's degree from Harvard University in 1899 and held a fellowship at the University of Chicago from 1900 to 1903. Adams was curator of the University of Michigan Museum from 1903 to 1906. He was director of the Cincinnati Society of Natural History from 1906 to 1907, and he was appointed curator of the University of Cincinnati Museum in 1907. Having obtained his doctorate, from 1908 to 1914 Adams was associate professor of animal ecology at the University of Illinois State Laboratory of Natural History. He was assistant professor of forest zoology at New York State College of Forestry, Syracuse, from 1914 to 1916, then professor of forest zoology until 1926, and from 1919 he was director of the Roosevelt Wildlife Forest Experiment Station. From 1926 to 1943, Adams was director of the New York State Museum in Albany. He died in Albany, New York, on May 22, 1955. Adams was one of the founders of the Ecological Society of America in 1916 and its president in 1923. In 1927 he was vice president of the Association of American Geographers.

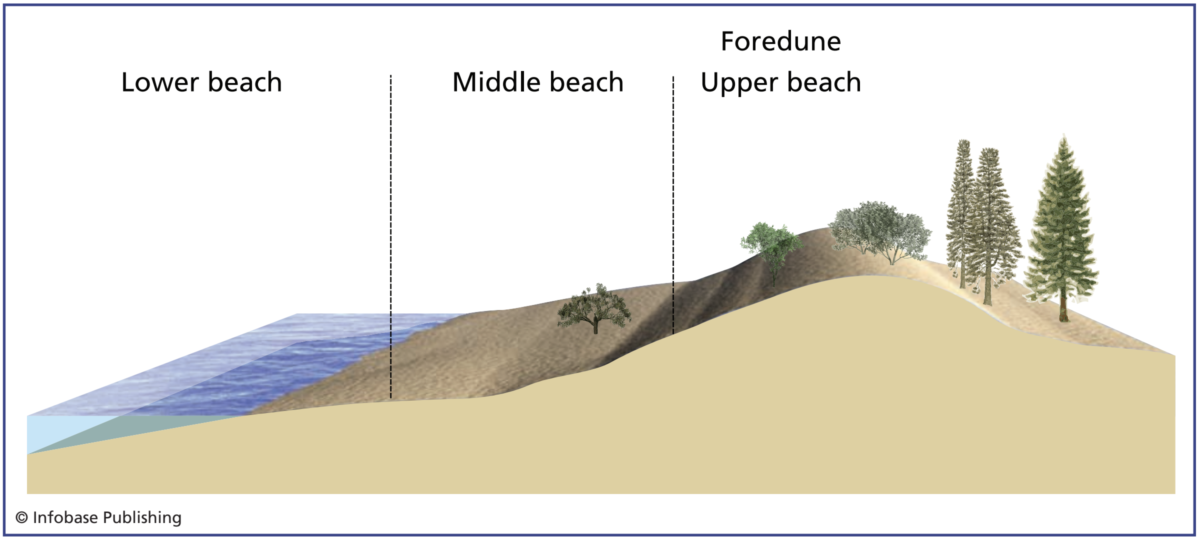
## HENRY CHANDLER COWLES AND THE SAND DUNES OF LAKE MICHIGAN

Sand dunes extend for some distance inshore along the southern and eastern coasts of Lake Michigan. The sand from which they are made once lay on the lake bed, at a time when the ice sheets of the last ice age were retreating and the water level was higher than it is today. Left high and dry by the retreating water level, storms and winds gradually threw the sand into the dunes.

Plants grow among the dunes, and willows and marsh plants grow in the *dune slacks*—flat-bottomed areas among the dunes where the water table is close to the surface. Tough grasses such as American marram grass (*Ammophila breviligulata*) have underground stems called *rhizomes* that bind the sand together, stabilizing the dunes and allowing other plants to establish themselves, after which the marram disappears. Marram rhizomes can grow several feet each year. But life is much harsher on the side of a dune facing the water—the *foredune.* There storm waves and gale-force winds blowing across the lake move the sand about, making it too unstable for most plants to find anchorage, even marram.

To an untrained eye the dune plants may appear to be scattered at random. Clumps of grass growing from hidden rhizomes are dotted here and there. Vegetation is abundant in some areas, sparse in some, and completely absent from others. The plant distribution is far from random, however, and the first biologist to study it carefully was a graduate student from the University of Chicago, Henry Chandler Cowles (1869–1939). Cowles was another pioneer of American ecology and the scientist who did much to popularize the term *ecology.* He was inspired to embark on his study of dune vegetation by reading Warming's book *Plantesamfund* (*see* "Eugenius Warming and the Ecology of Plants" on pages 136–138). The book had not yet been translated into English, so Cowles learned Danish in order to read it. Later, in 1905, he visited Warming in Copenhagen.

What Cowles discovered was that the proximity of the lake affected the type of plants that could grow on the dunes, especially on the foredunes. The lower part of the beach was battered by winter storms, alternately inundated with water and dried out by the Sun, and its sand shifted constantly. No plants survived there. The middle beach, fared better. It lay on the landward side of the lower beach, and in summer it was warm and beyond the reach of the waves. *Annual plants*—plants that complete their life cycle from germination to the production of seed and the death of their roots, stems, and leaves in a single year—thrived there. Longer-lived plants were washed away in




Plant distribution on the foredune—the side of the dune facing the water—forms distinct zones. There are no plants on the lower beach—the part of the sand dune that is washed by lake waves, especially during summer storms. Large waves can splash across the middle beach; there a few plants are able to survive. Plants thrive on the upper beach, beyond the reach of the waves.

winter. The annual plants were adapted to arid conditions, however, despite the proximity of the fresh lake water and the frequent rain. That is because the hot summer Sun and incessant wind dry out the sand and keep it dry, so it has a desert climate. Not even the winter storm waves could reach the upper beach, however, and there plants thrived. The diagram above illustrates the distribution Cowles found. Cowles was interested in plant life, but there is also animal life on the dunes, although the animals are small. Tiny invertebrates live in the moisture between sand grains, even on the lower beach, scavengers feed on dead fish and insects washed up by the waves, and predators hunt the scavengers.

Cowles wrote a full account of his sand dune research for his Ph.D. dissertation, and it was also published in 1899 in the University of Chicago's *Botanical Gazette* with the title "The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan." It became a classic in American ecological literature. Cowles went on to examine the plant ecology of the Chicago region; his paper "The Physiographic Ecology of Chicago and Vicinity" appeared in the *Botanical Gazette* in 1901. He wrote the second volume of *Text Book of Botany for Colleges and Universities,* published in two volumes in 1910–11 by the University of Chicago Press. In his volume, Cowles concentrated on autecology, and he was highly rigorous, refusing to allow that a plant had adapted to its way of life unless there was a good reason to believe that its characteristic features had evolved to perform the function they were now seen to perform. His great achievement, however, arose from his study of sand dunes: His study of the way plants were distributed on the dunes led him to the theory of ecological *succession*—the sequence of changes that takes place in a plant and animal community as the community adjusts to environmental changes or as new species arrive to alter its composition.

Henry Chandler Cowles was born on February 27, 1869, in Kensington, Connecticut. He studied geology at Oberlin College in Ohio, graduating in 1893, then taught natural science at Gates College, Nebraska, in 1894–95. In 1895 he moved to the University of Chicago to commence his graduate studies—and remained at the University of Chicago for the whole of his career. Cowles began there by studying geology, but he came under the influence of John Merle Coulter (1851–1928), the head of the university botany department and editor of the *Botanical Gazette* (and later author of the first volume of *Text Book of Botany for Colleges and Universities*). Coulter persuaded him to switch to botany. Cowles received his Ph.D. in 1898 for his sand dunes study and joined the botany faculty. He became professor of botany in 1911, and in 1925 he was made head of the botany department and editor of the *Botanical Gazette,* holding those positions until his retirement in 1934. Cowles helped found the Ecological Society of America in 1914 and was its president in 1917. In 1922 he was president of the Botanical Society of America. On his retirement he was made a life member of the British Ecological Society, and the following year (1935) the Ecological Society of America published a special issue of its journal *Ecology* in his honor.

Cowles lived at a time when academic scientists were not compelled to publish widely and frequently, and he wrote little. Instead, he devoted most of his effort to training and helping his graduate students. Cowles died in Chicago on September 12, 1939.

## FREDERIC E. CLEMENTS, PLANT SUCCESSION, AND THE SUPERORGANISM

In 1884 Charles Edwin Bessey (1845–1915) arrived in Lincoln, Nebraska, to take up the post of professor of botany at the University of Nebraska and Nebraska state botanist. He remained at the university for the rest of his life, becoming head dean of the Agricultural College in 1909. Bessey collected native Nebraska plants and exhibited them at the state fair, but his most memorable achievement was the planting of the Nebraska National Forest, in the Sandhills near Halsey. The forest nursery bears his name.

Bessey was very successful at teaching botany and promoting it as a science, but he was also a keen conservationist, especially concerned about the fate of the prairie grasslands. When the first European explorers moved westward into the interior of North America, they encountered a seemingly endless expanse of grassland. The types of dominant grasses varied according to the climate, with tall-grass prairie in the moister climate of the east, and short-grass prairie in the drier west. The tall grasses grew so high that only a person mounted on a horse could see the horizon. But settlers seeking land to farm soon followed the explorers, and by Bessey's time the original prairie was rapidly disappearing beneath the plow, and he feared all of it might soon be lost. It was not simply the loss of the appearance of the prairie that mattered to him, but of the prairie as a plant community. The photograph on page 147 of Minnesota short-grass prairie reveals just how many species of grasses, flowering herbs, and animals the prairie supports. The photograph also reveals another aspect of the prairie: its lack of features. Unlike an area of marsh beside a river, or an isolated patch of woodland, the prairie has no boundary.

The most famous of Bessey's students was Frederic E. Clements (1874–1945), who eventually became one of the most famous ecologists in the history of the science. Clements studied botany under Bessey and became interested in the ecology of the Nebraska grasslands. He and a fellow student, Nathan Roscoe Pound (1870–1964)—who later turned to law and became dean of Harvard Law School—decided in 1897 to undertake a formal ecological study of the prairie, along the lines set out by Oscar Drude (*see* "Oscar Drude and Plant Communities" on pages 132–133). Drude, a skilled botanist, could walk through

Bluestem prairie in a Nature Conservancy Preserve in Minnesota; this prairie contains 50 species of grasses, more than 250 species of flowering herbs, 20 species of butterflies, 70 species of birds, and 21 species of mammals. *(Jim Steinberg/Photo Researchers, Inc.)*

an area and obtain a reliable impression of its composition simply by observing it. He was working with European plant communities, however, and Clements and Pound quickly discovered that Drude's approach would not work on the boundless open prairie. If they were to learn the composition of the prairie vegetation, there was no other way than to bend down, identify the plants, and count the number of each species. It was a formidable task, but they found a way to simplify it by selecting small areas, which they called *quadrats.* They marked out the quadrats and counted the number of plants belonging to each species inside the boundary. Their quadrats varied in size, but most were 11 square feet ($1m^2$) in area, and to obtain a reliable sample they had to mark out many quadrats. Bessey, their teacher, had not been impressed by their plan to study grassland ecology. He did not believe ecology could ever become a properly rigorous science, but the method Clements and Pound devised convinced him otherwise. In 1898 Clements and Pound published their experiences and findings in *The Phytogeography of Nebraska,* which became a standard botany textbook, and in 1905 Clements described his research methods in *Research Methods in Ecology.*

Clements later continued his grassland studies in other parts of the western United States, and as he did so he was led to the observation that after an area of grassland had been disturbed the plants grew back in a definite order until they reached a mature, or *climax* state (*see* the sidebar on page 149). The stages by which the vegetation approached the climax struck him as similar to the stages by which an individual organism grows and matures. Seen in this light, the plant community might be likened to a single organism—a *superorganism.* Clements's concept of the superorganismic climax came to dominate ecological theory in the early years of the 20th century and enjoyed a revival toward the end of the century.

It was a rigid view that did not allow for gradual change over long periods. Clements was convinced that the prairie grassland had developed as a climax following the most recent ice age and that it would continue in its present form until the next major climatic shift. Should anything disturb the plant community, it would always retain the capacity to recover to its former state. Far from urging the restoration of the prairie, Clements was arguing that by understanding how plant communities develop—as superorganisms—it would be possible to manage agricultural plant communities. He sought to help the prairie farmers, not to stand in their way. Clements was not alone in this. The early ecologists accepted that human societies had no choice but to interfere with natural communities, and their aim was to ensure that the inevitable interference would be efficient, and therefore beneficial.

Frederic Edward Clements was born in Lincoln, Nebraska, on September 16, 1874, the son of Ephraim George Clements, a photographer and grandson of an immigrant from Somerset, England, and Mary Angeline Scoggin. Clements entered the University of Nebraska at the age of 16 and graduated in botany in 1894. He obtained a master's degree in 1896 and a Ph.D. in 1898. While a graduate student, Clements met Edith Gertrude Schwartz (1874–1971), a fellow botanist and ecologist, who received her Ph.D. in 1904. They were married on May 30, 1899. They had no children.

## THE CLIMAX CONCEPT

If all the vegetation is cleared from an area of land and the land is then left undisturbed, plants will start to appear before long. Light seeds, carried by the wind, will arrive first. These will germinate and grow into fast-growing flowering herbs. Larger seeds dropped by birds will produce more plants that grow rather more slowly, and finally the seeds that take longer to germinate will grow into larger, woody shrubs. Then, depending on the soil and climate, fast-growing trees may appear, followed by trees that grow more slowly. As the more substantial *perennial plants* grow up, they will shade the earlier ones and deprive them of nutrients, so the first arrivals will grow fast, set their seeds and release them to be carried by the wind to new sites, and disappear. As the years pass, the composition of the vegetation will change in a series of stages, or succession. Eventually, a plant community will emerge, with its associated animals, that is in a state of equilibrium with its physical and chemical environment and with the broader communities bordering it. Until some external event perturbs the community, it will continue to perpetuate itself, and any change in its composition will occur much more slowly than the successional changes that preceded its establishment. The community then constitutes a climax.

There are two possible types of climax concept: *monoclimax* and *polyclimax*. A monoclimax, originally proposed by F. E. Clements, follows a succession that leads to a definite type of plant community, its composition determined by the climate, and once the climax is reached, the vegetation pattern does not change. A polyclimax, originally proposed by A. G. Tansley, follows a succession that leads to a community that is in equilibrium with its environment, but its composition may be determined by factors other than climate—such as soil type or fire—and when a controlling factor changes—the climate changes or there is a fire, for instance—the vegetation will reach a new equilibrium, and hence a new climax, that may differ in composition from the earlier one.

Clements taught botany and plant physiology at the University of Nebraska from 1897 to 1907, when he became head of the botany department at the University of Minnesota, where he remained until 1917. From 1917 to 1925, he spent his winters working in Tucson, Arizona, at the desert laboratory of the Carnegie Institution, and from 1917 to 1941 he was a research associate in charge of ecological research for the Carnegie Institution. In 1925 he moved to the institution's coastal laboratory at Santa Barbara, California. Clements held many official positions. He was general secretary of the American Association for the Advancement of Science in 1910 and a consultant to the U.S. Soil Conservation Service 1934–45. Clements retired in 1941, but continued his research. He died in Santa Barbara on July 26, 1945.

## HENRY ALLAN GLEASON AND THE INDIVIDUALISTIC CONCEPT

Clements's concept of the succession and climax became less influential during the middle part of the 20th century, partly because Henry Allan Gleason (1882–1975) had proposed an alternative that many ecologists found more realistic. In fact, Gleason proposed his "individualistic hypothesis" as early as 1926 in a paper entitled "The Individualistic Concept of the Plant Association," which was published in the *Bulletin of the Torrey Botanical Club* (vol. 53, pp. 7–26), but at the time Gleason was not well known and Clements dominated the field.

Gleason studied the vegetation of his native Illinois, and he began his career using the methods Clements had developed, accepting the idea of a climax community as comprising a superorganism. After a time, however, he began to doubt the usefulness of Clements's theory. Clements assumed that a climax community would invariably comprise those species best adapted to the environment. That implied that in a particular environment there would always be the same species in the same relative proportions; if the vegetation were to be cleared, in time an identical plant community would occupy the site. Gleason rejected this, maintaining that plant communities vary continuously across environments that also vary continuously and, consequently, no two communities are identical. This makes it impossible, or at least very difficult, to put a name to a plant community, such as "oak–beech forest," because the name implies that all forests with that name are identical, which they are not. In his 1926 paper Gleason wrote the following:

> 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. The vegetation of an area is merely the resultant of two factors, the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment.

Gleason was saying that far from being a superorganism, the composition of a plant association is nothing more than a coincidence. If an area of land is cleared of vegetation, the composition of the vegetation that comes to fill it depends on which seeds just happen to fall onto the ground and germinate and in which order plants chance to arrive. The distribution of plants is not far short of being random.

Frustrated because most other ecologists ignored his ideas, Gleason abandoned ecology and became a plant taxonomist—eventually a highly skilled and greatly respected one—working at the New York Botanical Garden. His individualistic hypothesis aroused much debate in the 1950s and 1960s, when Darwinian evolutionary theory merged with the growing understanding of heredity to produce what became known as the modern synthesis. The modern synthesis was extremely influential among biologists, and it favored Gleason's individualistic hypothesis. Gleason's idea still remains influential, although it has been somewhat moderated. Today the most widely held version of the Gleason hypothesis states that evolutionary processes in the past may have influenced the composition and structure of present communities, but they can shed no light on the consequences of disturbance and are therefore of no ecological value.

Henry Allan Gleason was born on January 2, 1882, on a farm near Dalton City, Illinois. His home was somewhat isolated, and during his early childhood there were no other boys nearby with whom he could make friends. When he was nearly 11, the family moved to Decatur, Illinois, where there were other boys, but Gleason had no experience in forming relationships with them. The new family home was at the edge of the city, and Gleason spent much of his time in nearby woods, where he met other boys who preferred to be in the countryside. It is where he acquired and developed his love of plants and animals. When he was 13, he took a botany course at Decatur High School, and while still at high school he sent an account of the local naturalization of a plant from a single original planting to Charles Bessey, who was then editor of *The American Naturalist.* Bessey published it in 1897. Gleason went on to study botany at the University of Illinois, graduating in 1901 and earning a master's degree in 1904. He received his Ph.D. from Columbia University in 1906 for work on the taxonomy of *Trillium,* a genus of 42 species of North American plants. Gleason taught at the universities of Illinois and Michigan, then spent a year studying the plants of the Philippines, Java, and Sri Lanka. On his return, in 1918 Gleason described his findings in a lecture to the Torrey Botanical Club, as a result of which he was offered a permanent position at the New York Botanical Garden, where he worked from 1918 until 1950.

In 1915 Gleason married Eleanor Theodolinda Mattei, one of his Michigan students. They had three children. Gleason died in New York on April 12, 1975.

## VICTOR E. SHELFORD AND ANIMAL COMMUNITIES

Clements never responded directly to Gleason's criticism, but by the late 1930s he had become less insistent on studying communities as single entities, the approach that had led him to the idea of a community as a superorganism. In *Bio-Ecology,* the book Clements wrote in collaboration with Victor E. Shelford (1877–1968) and that was published in 1939, Clements used the term *superorganism* as a synonym for "a complex organism with characteristic development and structure."

In *Bio-Ecology* the two authors brought plant and animal communities together and considered aquatic as well as terrestrial communities. The inclusion of animals was Shelford's contribution. By considering plants and animals together, Clements and Shelford were able to develop the concept of the biome, a term Clements had coined, first using it in December 1916 at a meeting in New York of the Ecological Society of America.

Shelford began his career as a zoologist and became an animal ecologist in the 1920s, when he began to apply the concepts of succession, community, and climax to animals. It was this work that launched the subject of animal ecology, and Shelford is sometimes called the father of that discipline. In addition to *Bio-Ecology,* Shelford wrote two major works: *Animal Communities in Temperate America as Illustrated in the Chicago Region,* published in 1913, and *The Ecology of North America,* published in 1963. Shelford had been a student of Henry C. Cowles (*see* "Henry Chandler Cowles and the Sand Dunes of Lake Michigan" on pages 142–145), and the research he undertook for his Ph.D. was on the tiger beetles that inhabit sand dunes, a topic of considerable interest to Cowles.

Victor Ernest Shelford was born on September 22, 1877, at Chemung, New York. He attended local schools and in 1894 began teaching at public schools in Chemung County. After studying for two years, he obtained a teaching certificate at the Cortland Normal and Training School, and in 1897 he returned to teaching. In 1899 he enrolled at West Virginia University to study zoology. In 1901 the president of West Virginia University, Jerome H. Raymond, was appointed a professor at the University of Chicago, and Raymond helped Shelford obtain a scholarship. Shelford transferred to the University of Chicago in 1901, and he taught zoology there as an instructor from 1903 to 1914. He obtained his Ph.D. in 1907 at the University of Chicago. In 1914 Shelford moved to the University of Illinois, and along with his university research and teaching commitments, from 1914 to 1929 he was the biologist in charge of the research laboratories of the Illinois Natural History Survey. In alternate summers from 1914 to 1930, Shelford was also director of marine ecology at the Puget Sound Biological Station. He became professor of zoology at the University of Illinois in 1927, remaining in this post until 1946.

Shelford helped found the Ecological Society of America (ESA) in 1915 and was its president in 1916. He was a keen conservationist, and this involved him in a conflict within the ESA. Some members believed the society should exist only to support ecologists, while others said that it should take a more active part in conserving habitats that were at risk. Shelford supported the conservationists, and in 1917 he formed an activist wing of the ESA, the Committee for the Preservation of Natural Conditions. Shelford helped compile *A Naturalist's Guide to the Americas,* which the ESA published in 1926. This work attempted to list all the known areas of undisturbed habitat in North America and parts of Latin America. In 1946 the committee became the Ecologists' Union, and in 1950 it changed its name to the Nature Conservancy. Shelford helped establish the Grassland Research Foundation in 1939 and was its president in 1958.

Shelford married Mary Mabel Brown in 1907. They had two children. Shelford died in Urbana, Illinois, on December 27, 1968.

## ROBERT H. MACARTHUR AND THE TESTING OF HYPOTHESES

The English-born American zoologist and ecologist G. Evelyn Hutchinson (1903–91) was one of the first ecologists to suggest that a community of plants and animals might be considered as a *system* regulated by interactions among its members. A system is a group of objects that work together in such a way that a change in one of the objects affects the group as a whole. An engine is a system—all of its components are different, and if a component fails, the engine loses power or stops. The control within the system is exercised by feedbacks. For example, if prey numbers increase, predators will have more food, so their numbers will also increase. The predators will then eat more prey, reducing prey numbers, and the reduction in prey numbers will cause a proportionate reduction in predator numbers. This set of events constitutes a feedback, in this case a negative feedback because it restores the original situation. In suggesting that a biological community might constitute a system, Hutchinson may seem to have been reviving Clements's concept of a superorganism—and perhaps foreshadowing Lovelock's Gaia hypothesis (*see* "James Lovelock and the Physiology of the Earth" on pages 108–112)—but his idea was much more mechanistic. In his view, community relationships were essentially economic.

One of Hutchinson's students, Robert MacArthur (1930–72), went on to develop Hutchinson's suggestion, and in doing so he initiated another new discipline: *community ecology.* Community ecology is the study of the relationships within a biological community, classifying and arranging them in order, to determine how members of the community interact. In 1958, for his Ph.D. research, MacArthur showed that five similar species of insect-eating warblers in a New York coniferous wood fed in different parts of the trees. This provided direct support for the competitive exclusion principle by showing that these similar species were not, in fact, competing. MacArthur also developed mathematical models of ecological relationships, thus bringing much more precision to what had previously been fairly general ideas.

In all of his studies MacArthur emphasized the importance of testing hypotheses statistically. By this he meant that an experimenter seeking to determine whether experimental data confirm a particular interpretation should begin by assuming the opposite of the expected result, called the *null hypothesis.* The implications of the null hypothesis are then compared to the experimental data. If the data agree with the null hypothesis, then the null hypothesis is likely to be correct; if they do not, then some other factor must be invoked to explain them. Other mathematicians later developed this approach further, and it is now one of the most widely used techniques for evaluating ecological data.

His mathematical models made MacArthur one of the most influential ecologists of his generation. They enabled him to find possible answers to questions that no one had asked before, such as whether the size of a population was determined by its physical environment or by competition for resources, and whether the *niche* a species occupies changes as the occupant adapts to its surroundings. A niche is the function an organism fulfils in its environment, including the frequency with which it is present in a particular habitat and the amount of time it spends there, and the resources it utilizes. MacArthur helped to formulate the *optimum foraging theory,* which proposes that as an animal moves across its territory in search of food it makes decisions that maximize the amount of food it finds or that improve its foraging efficiency in some other way.

MacArthur also collaborated with the ecologist E. O. Wilson (1929– ) in advancing the theory of *island biogeography,* which states that the number of species on an island is determined by immigration from the nearest mainland and extinction; when these reach equilibrium, the total remains constant although the composition of the community changes. The theory was later found to be too simplistic, and it has largely been abandoned, but it aroused much interest when *The Theory of Island Biogeography,* their book describing it, was first published in 1967, and it threw considerable light on what happens when changes in land use break areas of habitat into fragments and on how best to plan nature reserves.

Robert Helmer MacArthur was born on April 7, 1930, in Vermont. He studied at Marlboro College, in Marlboro, Vermont, and obtained his master's degree in mathematics from Brown University in 1953. He then moved to Yale University, where he conducted the research for his Ph.D. under the supervision of Hutchinson. He received his Ph.D. from Yale in 1958. MacArthur was a professor at the University of Pennsylvania 1958–65 and professor of biology at Princeton University from 1965 until his death. He died from renal cancer on November 1, 1972.

## ALFRED J. LOTKA, VITO VOLTERRA, AND THE MATHEMATICS OF RELATIONSHIPS

Mathematicians had been studying the way animal populations change since the 1920s. The American physical chemist and mathematician Alfred J. Lotka (1880–1949) wrote a book on the mathematics of populations entitled *Elements of Physical Biology,* which was published in 1925 and reprinted in 1956 with a new title: *Elements of Mathematical Biology.* Lotka's idea was that the process of evolution by natural selection could be described mathematically, in the same way as a physical law. He thought this might be possible because food and other resources represent energy—food values are measured in joules or calories, which are units of energy—and natural selection favors those individuals that are most efficient at obtaining energy, utilizing it metabolically, and making a proportion of it available to their offspring. In working this idea through, Lotka explored a range of related problems, including energy balances, the mathematics of growth and reproduction, the equilibrium that organisms reach with their environment, the operations of the senses, and consciousness.

Lotka's mathematics aroused only minor interest among ecologists until, in 1926, the Italian physicist and mathematician Vito Volterra (1860–1940) became interested in the problem of calculating the size of fish stocks and the size of the catch a fishing fleet could take without depleting the population. Fishing boats are effectively predators, and Volterra was able to calculate a way to express mathematically the relationship between the population sizes of predators and their prey. He based his mathematics partly on the physical theory governing the frequency with which molecules in a gas collide with one another.

Volterra also applied an equation formulated in 1846 by the Belgian mathematician Pierre François Verhulst (1804–49) that had been rediscovered in 1920 by the American population geneticist Raymond Pearl (1879–1940). Verhulst's equation, now called the *logistic equation,* made it possible to calculate the rate at which a population grows toward the *carrying capacity*—the largest number of individuals an environment with limited resources can support. The equation is: $dN/dT = rN((K-N)/K)$, where $N$ is the number of individuals, $T$ is time, $r$ is the rate at which the population is capable of increasing, and $K$ is the carrying capacity of the environment; $dN/dT$ represents the rate of population growth. The expression $K-N/K$ ensures that the rate of population growth slows as the size of the population ($N$) approaches the carrying capacity ($K$).

When Lotka's and Volterra's equations were combined, they formed the Lotka–Volterra equations. These describe the competition between species living in the same area and with similar environmental requirements, as well as simple relationships between predators and prey. They are the equations the Russian biologist G. F. Gause tested a few years later, deriving from them the competitive exclusion principle (*see* "G. F. Gause and the Struggle for Existence" on pages 112–114).

Alfred James Lotka was born on March 2, 1880, in Lemberg, Austria-Hungary (now Lwiw, Ukraine). His parents were American missionaries. He studied at the University of Birmingham, England, where he obtained his B.Sc. degree in 1901, then spent some time at the University of Leipzig, Germany, before moving to the United States, where he worked for the General Chemical Company from 1902 to 1908. He received his master's degree in physics from Cornell University in 1909, then became an examiner at the U.S. Patent Office for a few months before moving to the U.S. Bureau of Standards, where he worked as an assistant physicist from 1909 to 1911. He received his doctor of science degree in 1912 from the University of Birmingham, and in subsequent years he worked at the General Chemical Company and Johns Hopkins University, before joining the Metropolitan Life Insurance Company as supervisor of its statistical bureau, where he remained until his retirement in 1948. He was president of the Population Association of America 1938–39, and of the American Statistical Association in 1942. He died in Red Bank, New Jersey, on December 5, 1949.

Vito Volterra was born on May 3, 1860, at Ancona, Papal States (which were absorbed into the Kingdom of Italy in 1870), into a poor Jewish family. His father died when he was two. Volterra showed early mathematical promise and was able to enroll at the University of Pisa in 1878. He graduated in 1882 as a doctor of physics, and the following year he became professor of rational mechanics at Pisa. In 1883 Volterra became professor of mathematical physics. He was later made professor of mechanics at the University of Turin, and in 1900 he was appointed professor of mathematical physics at the University of Rome La Sapienza. He served in the Italian air force during World War I, working on airship designs, and returned to the University of Rome when the war ended.

Volterra was elected to the Italian Senate in 1905. Passionately democratic, following the rise to power of the Fascists in 1922, he was a principal signatory of the Intellectuals' Declaration Against Fascism. At the time he was president of the Accademia dei Lincei, the leading Italian scientific society and a post once held by Galileo, so his support was highly influential. Parliament was abolished in 1930, and in 1931 university professors were required to take an oath of loyalty to the Fascist government. Of the 1,250 professors approached, only 12 refused; Volterra was one. His refusal meant he had to resign from the university, and in 1931 he had to leave all his scientific posts. He moved abroad, living in Paris and Spain, and returned to Rome shortly before his death on October 11, 1940.

## RAYMOND LINDEMAN, ENERGY AND EFFICIENCY

In 1942, a few months after its author's death, the journal *Ecology* published a paper by the American ecologist Raymond Lindeman (1915–42), entitled "The Trophic–Dynamic Aspect of Ecology." Lindeman's final paper analyzes the flow of energy through a community. Green plants manufacture carbohydrates by photosynthesis, and carbohydrates represent chemical energy. Herbivorous animals consume green plants, and therefore assimilate a proportion of that energy. Carnivorous animals feed on herbivores, assimilating a proportion of the energy the herbivores obtained from their food. Lindeman had found a way to track that flow of energy and calculate the proportion that passed from each *trophic*—pertaining to food or nutrition—level to the next.

Lindeman had shown a way to unite autecology and synecology, the two main strands of ecology. Autecology is the study of the ecology of individual organisms and populations, synecology of entire communities. Lindeman began his analysis by recognizing that sunlight is the original source of all the energy available to living organisms. Photosynthesis captures a measurable amount of that solar energy. Green plants use some of the energy they have captured to drive their own metabolism—the growth and repair of plant tissues, the production of flowers, fruits, and seeds, and so forth. The proportion of absorbed energy that accumulates in edible plant tissue such as leaves and stems is called *production,* and green plants are described as *producers.* An animal that feeds on the producers is, therefore, a *consumer*—a *primary consumer* if it feeds on plants, a *secondary consumer* if it feeds on herbivorous animals, and a *tertiary consumer* if it feeds on carnivores. Consumers use much of the energy they absorb from their food to maintain their own metabolism. All organisms, producers and consumers, release energy by the process of *respiration,* which is the reverse of photosynthesis, in other words it is a sequence of chemical reactions in which an organism oxidizes organic compounds with the release of energy, as the following two equations show.

Photosynthesis: $6CO_2 + 6H_2O \rightarrow C_6H_{12}O_6 + H_2O + 6O_2 \uparrow$

Respiration: $C_6H_{12}O_6 + 6O_2 \rightarrow 6H_2O + 6CO_2 \uparrow$

$C_6H_{12}O_6$ is glucose, a simple sugar, and the arrows pointing upward mean the gases oxygen ($O_2$) and carbon dioxide ($CO_2$) are released into the air.

When organisms shed waste products and finally die, the resulting dead organic material provides food—and energy—for another hierarchy of organisms. The processes of photosynthesis and respiration involve the absorption and release of energy. Using energy as a measure—just as one might use the flow of money—Lindeman had made it possible to measure the economics and energy efficiency of relationships within the trophic levels of ecosystems.

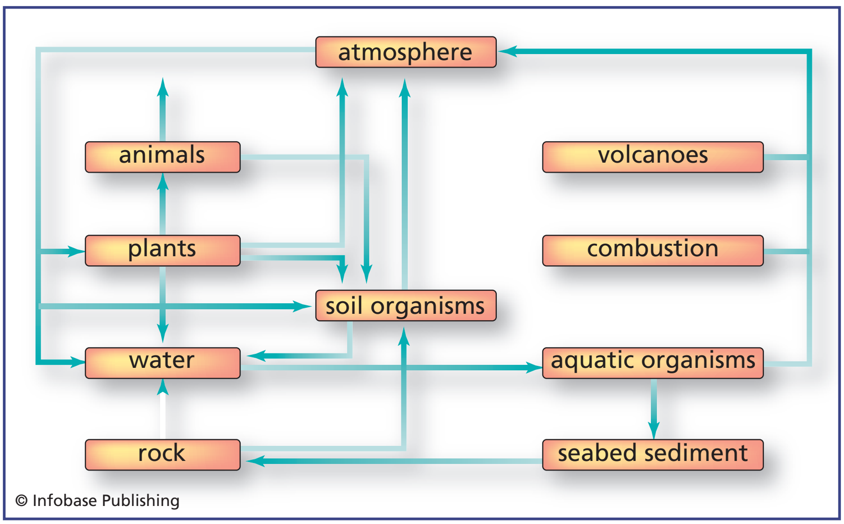
It was a major breakthrough. Soon after his death, G. Evelyn Hutchinson, his senior colleague at Yale University, described Lindeman as "one of the most creative and generous minds yet to devote itself to ecological science." Hutchinson studied aquatic ecosystems, and the ecosystem Lindeman studied was in Cedar Bog Lake, in what is now the University of Minnesota's Cedar Creek Ecosystem Science Reserve. In 1982 ASLO (the American Society of Limnology and Oceanography) instituted an annual award for excellence in any branch of limnology or oceanography in honor of G. Evelyn Hutchinson. In 1987 it instituted another award, made annually to the author of an outstanding paper written by a young aquatic scientist, to honor Raymond L. Lindeman.

Raymond Laurel Lindeman graduated and completed his Ph.D. at the University of Minnesota. He then moved to Yale, where he conducted postdoctoral research under the supervision of G. Evelyn Hutchinson. Lindeman published only five scientific papers before his death at the age of 27 from a rare form of hepatitis. His final paper was published posthumously.

## THE ODUM BROTHERS AND SYSTEMS ECOLOGY

Air contains carbon dioxide. Green plants and certain bacteria absorb this gas from the air and use its carbon to synthesize carbohydrates. Animals consume the carbohydrates. Both plants and animals respire, and respiration, the reverse of photosynthesis, returns carbon dioxide to the air. The burning of any substance containing carbon also releases carbon dioxide into the air. Gases released by erupting volcanoes are the original source of all this carbon dioxide, and a proportion of the carbon in aquatic organisms sinks to the seabed, where it joins the sediment and eventually is converted to sedimentary rock—called *carbonate rock* because it contains carbon. The element carbon circulates ceaselessly between rocks, water, air, and living organisms. The illustration below is a simplified diagram of the carbon cycle. Several other elements that plants and animals utilize as nutrients also cycle in this way in what are called *biogeochemical cycles.*

Howard Thomas Odum (1924–2002), another of G. Evelyn Hutchinson's graduate students at Yale University, was the first scientist to draw attention to the cycling of elements. Odum's doctoral



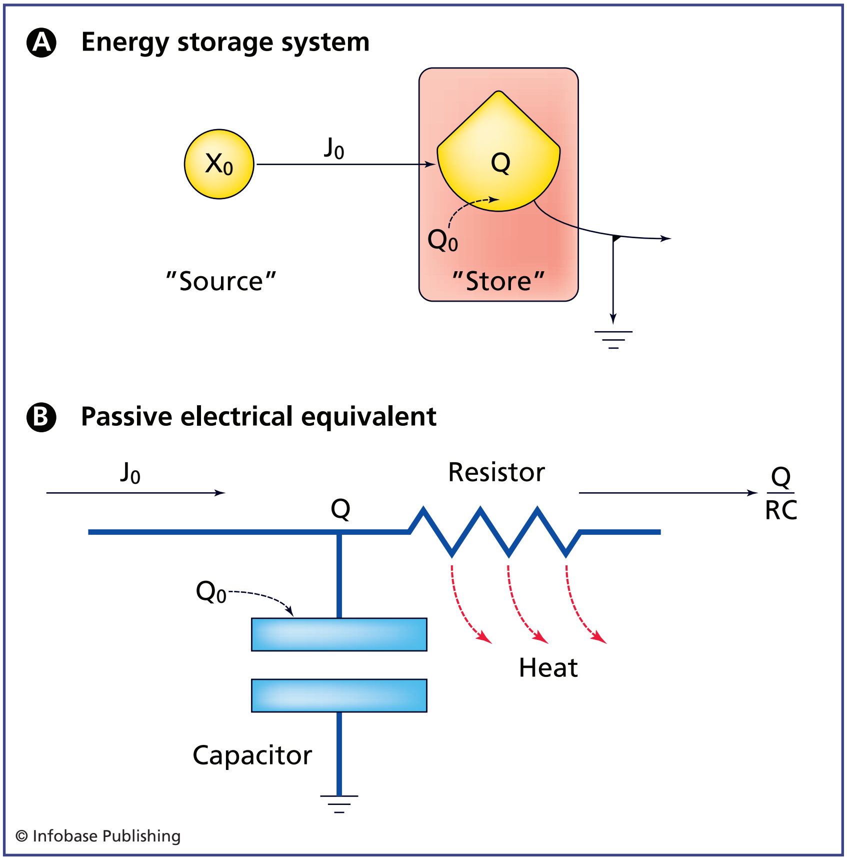

Volcanoes and the weathering of carbonate rocks release carbon into the atmosphere. Plants absorb carbon, and animals obtain carbon from plants. Respiration by plants and animals returns carbon to the air, and some carbon sinks to the seabed, where eventually it forms sedimentary rock.

thesis, which he wrote in 1950, was entitled *The Biogeochemistry of Strontium: With Discussion on the Ecological Integration of Elements.* Odum had initially been interested mainly in ornithology, but with his doctoral research his career changed direction because his study of biogeochemistry had profound implications. It demonstrated that no community of plants and animals can ever be thought of as isolated because the chemical elements from which it is made travel by air and water all over the world. These elemental cycles link ecosystems together into a single ecosystem spanning the entire planet, the concept of a unity of living organisms originally proposed by Vernadsky (*see* "Vladimir Vernadsky and the Discovery of the Biosphere" on pages 106–108).

Howard Odum took Vernadsky's idea further, into *systems ecology*—the branch of ecology that studies ecosystems as complex systems regulated by feedbacks and with characteristics that cannot be deduced from the study of the individual components of the system. He was especially interested in the transfer of energy from one organism to another through ecosystems, representing this with flow diagrams similar to those used in other branches of the study of general systems. The illustration on page 162 shows an example of the type of diagrams Odum used. Odum devised a set of symbols for use in his diagrams, shown in the illustration on page 163. These represented stages—such as "source," "store," "consumption," and "interaction"—in the flow of energy through a system. Lines linking the symbols traced the entire flow. Odum called the symbols and this use of them "energese," as though it were a language. He wrote the chapter on energy flow through systems, which he called "energetics," in *Fundamentals of Ecology,* the textbook on systems ecology he wrote in collaboration with his elder brother, Eugene (1913–2002), published in 1953.

While Howard wrote the chapter on energetics, Eugene Odum wrote the remainder of their book. Eugene promoted the use of the term *ecosystem,* which had been defined earlier by the British ecologist Arthur G. Tansley (*see* "Arthur G. Tansley, Exploring British Plants" on pages 166–170), and made it central to his view of ecology.

During the 1950s, the U.S. government began commissioning environmental studies of sites they planned to develop for nuclear weapons production, and in 1951 Eugene Odum obtained a grant to conduct such a study of the Savannah River site in South Carolina, Howard Odum developed a way to represent an energy storage system (top) using a diagram similar to those used to describe a passive electrical equivalent system (bottom).

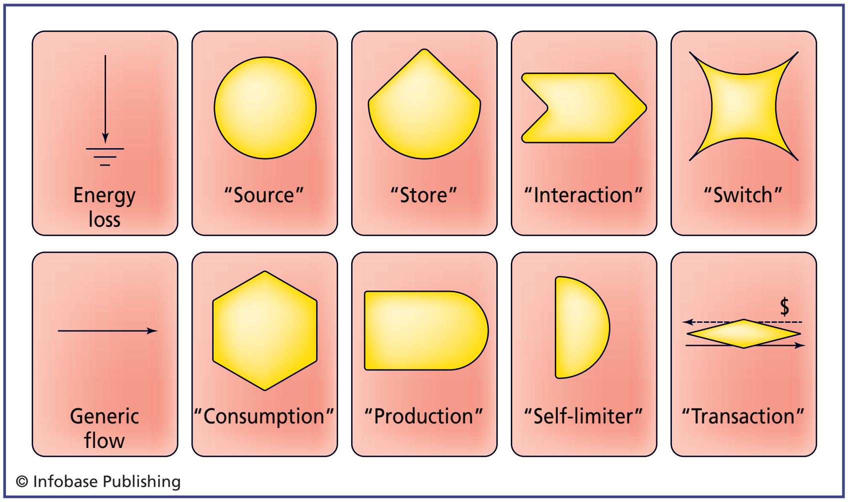



where a plant was to be built for producing weapons-grade nuclear material. The program Odum and his students began there grew into the Savannah River Ecology Laboratory. In 1954 Eugene and Howard collaborated in another study, this time of the effects of nuclear weapons testing on Eniwetok Atoll, in the South Pacific Ocean. In the course of that study, the Odums discovered that the coral reef was maintaining itself because of a *symbiosis*—a situation in which two dissimilar organisms live together in close association—between the coral and algae that performed photosynthesis.

Starting in the 1960s, increasing popular concern about the condition of the natural environment and the harm being caused by pollution led many members of the emerging environmental movement to interest themselves in ecology (*see* "Ecology and Environmentalism" on pages 186–198). Eugene Odum became a highly influential figure in that movement through his explanations of ecological principles and his firm belief in the possibility of human societies living more harmoniously within the natural environment. He was always a scientist, however, and never what would nowadays be called an environmental activist.

The Odum brothers were the sons of Howard Washington Odum (1884–1954), an American sociologist, and Anna Louise Kranz. Eugene Pleasants Odum was born on September 17, 1913, at Newport, New Hampshire, where his parents were vacationing. His father was then on the faculty of the University of Georgia. The family later moved to Chapel Hill, North Carolina, and Eugene studied at the University of North Carolina, graduating in zoology with a bachelor's degree in 1934 and master's degree in 1936. He then moved to the University of Illinois, where he received his Ph.D. in zoology and ecology in 1939. He was resident naturalist at a nature preserve in New York in 1939–40, and in 1940 he joined the zoology department at the University of Georgia. He remained at the University of Georgia until he retired in 1984. He married Martha Ann Huff in 1939. They had two sons. Eugene Odum died at Athens, Georgia, on August 10, 2002.

Howard Thomas Odum was born on September 1, 1924, at Chapel Hill, North Carolina, where his father was a professor of sociology at the University of North Carolina. Howard grew up with his sister,




Howard Odum devised a set of symbols to represent events within ecosystems. He called this use of symbols "energese."

Mary Frances, and his, brother Eugene. Eugene taught him how to watch and identify birds, stimulating his interest in ornithology. Howard studied zoology at the University of North Carolina, but interrupted his studies to serve as a meteorologist in the U.S. Army Air Corps during World War II. He graduated in 1947 and received his Ph.D. from Yale University in 1950. He was director of the Marine Institute of the University of Texas from 1956 to 1963, when he joined the zoology department at the University of North Carolina. In 1970 he moved to the University of Florida, where he remained until he retired in 1996. Howard married twice. He and his first wife, Virginia Wood, had two children. She died in 1973, and the following year Howard married Elizabeth C. Odum, who had four children from a previous marriage. Odum died in Gainesville, Florida, on September 11, 2002.

9

# British Ecology

There are very few areas in Great Britain—and those are quite small—that have not been modified by human activity. Even the Scottish Highlands, which today is a large (for Britain), sparsely populated mountainous region, dominated by heather and bracken, once supported a much larger human population. Its better land was farmed, and livestock grazed its lower slopes. Lowland Britain has been farmed for many centuries, some of it since Neolithic times, and during the Roman occupation Britain exported grain to Rome.

As the science of ecology developed, therefore, British ecologists found themselves in a very different position from their American colleagues. Frederic E. Clements (*see* "Frederic E. Clements, Plant Succession, and the Superorganism" on pages 146–149) based his theory of a succession leading to a climax on his studies of the prairie, and his conclusions contained a hidden assumption that many environmentalists now take for granted: that a natural climax is inherently superior to any type of vegetation resulting from human intervention. This assumption presented British ecologists with a problem. The United States has a population density of 85.6 persons per square mile (33 per $km^2$). The United Kingdom, which includes mainland Great Britain, Northern Ireland, and many offshore islands, has a population density of 650.1 persons per square mile (251 per $km^2$). Until modern times, a poor harvest meant hunger for many and possibly starvation for some, and an attractive landscape was one that produced abundant food. Consequently, British ecologists tended to reject the idea of a natural climax as being superior to a managed type of vegetation. Had they accepted it, they would have found themselves urging the abandonment of agriculture and forestry over large areas.

That does not mean that British ecologists were opposed to conservation—far from it. But their approach to wildlife conservation involved them in the design of nature reserves, of limited extent and in some cases very small indeed, to provide habitat for particular species or to preserve certain plant communities. The reserves then had to be managed if the communities and species were not to be overwhelmed by more aggressive competitors arriving as components of a succession leading to a natural climax.

This short chapter outlines the development of ecology in Britain. It concentrates on three of the most important figures in that development. Arthur G. Tansley used ecology as a way of approaching botany by studying plants in their natural environment. Charles Elton advanced the study of animal ecology. R. A. Fisher was a statistician and geneticist who pioneered the application of statistical techniques to ecological studies.

## ARTHUR G. TANSLEY, EXPLORING BRITISH PLANTS

Arthur G. Tansley (1871–1955) was one of the most influential ecologists of the 20th century. He did much to make ecology a professional scientific discipline, and he was a talented writer and highly effective teacher. In particular, he moved ecological thinking away from loosely defined comparisons with human societies by insisting on strict definitions and a concentration on the flow of energy and chemical nutrients. Although he often used them, Tansley disapproved of employing words such as *community* and *neighborhood* to describe groups of plant and animals and their spatial arrangement. He thought it inappropriate to speak and write of nonhumans in language reminiscent of human societies. Tansley also objected to *organism* when applied to both plants and animals because plants and animals are so different from one another.

Nor did Tansley accept the assumed superiority of the climax superorganism Clements had proposed, although he approved strongly of the general scheme Clements had described in his 1916 book, *Plant Succession.* In the preface to his own textbook, *Practical*

*Plant Ecology*, published in 1923 and in a revised edition as *Introduction to Plant Ecology* in 1946, Tansley wrote the following:

> The chief climax units of vegetation—association, consociation and society—are adopted from Clements's scheme. They seem to the author the most satisfactory working units, and they have been taken up and successfully used by several of the best recent British workers. The conception of a climax is not, however, restricted to the climatic climax, but is applied to any relatively stable and well characterised community determined by any actual combination of persistent factors, including biotic factors.

Tansley advised his readers to begin their study of ecology by studying plant ecology, which he suggested was more easily approached than any other branch of the subject, but the influence of animals, including humans, must be included. "Man," he wrote, "occupies a unique position owing to his far-extended control over nature." This led him to the following passage, in which he expresses a European view that differs from the Clementsian vision of the original, vast, unspoiled prairie:

> Thus anything like a *complete* study of the ecology of a plant community necessarily includes a study of the animals living in or feeding upon it. The influence of man upon plant communities is of first importance in all but the most uninhabited and the most sparsely inhabited regions of the earth. . . . we can never afford to lose sight of past and present human activities in their effects on the vegetation of countries which have long been inhabited and densely populated, like those of Western and Central Europe.

In the 1946 revised edition, Tansley explained the concept of the ecosystem. He used the term *biome* in a different sense from the modern one, using it to describe "the whole complex of organisms—both animal and plants—naturally living together as a sociological unit," and continues:

> A wider conception still is to include with the biome all the physical and chemical factors of the biome's environment or habitat—those factors which we have considered under the headings of climate

> and soil—as parts of one physical *system,* which we may call an *ecosystem,* because it is based on the *oikos* or home of a particular biome.

Tansley first used the term *ecosystem* in “The Use and Abuse of Vegetational Concepts and Terms,” an article published in the journal *Ecology* in 1935, but he did not coin the word. It was first used in 1930 by the British botanist Arthur Roy Clapham (1904–90) in response to an inquiry by Tansley, who had asked him to think of a word to describe the physical, chemical, and biological components of an environment when these are considered together.

Arthur George Tansley was born in London on August 15, 1871. He attended Highgate School from 1886 until early 1889, when he studied science at University College, London. In 1890 he entered Trinity College, University of Cambridge, to study botany, graduating in 1894. He combined his Cambridge studies with teaching at University College, London, between 1893 and 1895 (London and Cambridge are a short train journey apart). After graduating from Cambridge, he returned to University College as a demonstrator in botany and assistant to his former teacher, Francis Oliver.

Tansley spent the years 1900 and 1901 studying the plants of Egypt, Sri Lanka, and the Malay Peninsula. On his return to Britain, Tansley found he needed to raise public support in order to obtain the funding needed to establish ecology as a discipline. In 1902 he founded *The New Phytologist*—*phytology* is the study of plants. He was editor of this journal from its first issue until 1931. In 1907 Tansley became a lecturer in botany at Cambridge, where he remained until 1923. He had grown interested in psychology, and in 1923 he resigned from Cambridge and spent a year in Vienna studying under Sigmund Freud. In 1927 Tansley was appointed Sherardian Professor of Botany at the University of Oxford, where he remained until he retired in 1939.

In 1904, in collaboration with the Scottish botanist William Wright Smith (1875–1956), Tansley established the Committee for the Survey and Study of British Vegetation. For many years Smith was regius professor of botany at the University of Edinburgh, regius keeper of the Royal Botanic Garden, Edinburgh, and Queen’s botanist in Scotland. From 1944 to 1949, he was president of the Royal Society of Edinburgh. The committee later condensed its name to the

British Vegetation Committee. The committee's aim was to map the entire vegetation of the British Isles, and in 1911 the team of scientists engaged in the task published their results in *Types of British Vegetation,* edited by Tansley, who was also a major contributor.

*Types of British Vegetation* was a substantial achievement, but the scientists who wrote it were dissatisfied and, in order to support and provide a forum for ecologists, on April 12, 1913, they founded the British Ecological Society, with Tansley as its first president. In 1916 the society founded the *Journal of Ecology,* which Tansley edited until 1938.

Tansley later expanded on *Types of British Vegetation* by showing how a wide range of factors, including past and present human activities, affects the vegetation of an area. He also conducted a review of all the existing accounts of British vegetation and linked these themes to show how the external factors had produced the patterns of vegetation the book described. Tansley published this in 1939 with the title *The British Islands and Their Vegetation.* It was his major single literary achievement. In 1949 he published a shorter version, with the title *Britain's Green Mantle.*

During the first half of the 20th century, popular pressure grew across Europe for the conservation of natural habitats and the species inhabiting them. It was impossible to establish in Britain huge national parks and refuges like those in the United States, and instead smaller areas were designated as nature reserves. This designation protected them from encroachment by industrial or housing developments, and by the end of World War II Britain had enough reserves to justify the government in forming a Wild Life Conservation Committee to identify other areas that might be made into reserves. Tansley had argued for more reserves in his book *Our Heritage of Wild Nature,* published in 1945. Julian Huxley (1887–1975) was the first chairman of the committee, but in 1946 he left to head the newly formed UNESCO (United Nations Educational, Scientific, and Cultural Organization), and Tansley took his place. In 1949 the government established the Nature Conservancy (now called Natural England), chaired by Tansley, to manage the state-owned nature reserves in England and promote ecological research. Tansley remained its chairman until 1953. From 1947 until 1953, Tansley was also president of the Council for the Promotion of Field Studies (now the Field Studies Council).

Arthur Tansley was elected a fellow of the Royal Society in 1915. In 1941 he was awarded the gold medal of the Linnean Society. He was knighted in 1950. Sir Arthur Tansley died at Grantchester, near Cambridge, on November 25, 1955.

## CHARLES ELTON, REGULATING POPULATIONS

Rats and mice are serious pests. They find their way into food stores, consume large amounts of the contents, and contaminate what they do not eat. They also transmit infections to humans. Rabbits are also serious pests in Britain. They feed on grassland that would otherwise be feeding cattle and sheep for human consumption. This has been the case for many centuries, but at the outset of World War II the situation became serious. In 1939, when the war began, the United Kingdom imported 60 percent of its food, and the country was threatened by a German naval blockade of its ports and attacks on merchant ships bound for them. Seeking ways to control these pest populations, the government's Agricultural Research Council turned for help to the Bureau of Animal Population at the University of Oxford. The international team of scientists at the bureau proposed control methods that prevented food losses that might have added greatly to the hardship British people were suffering, for food rations were already meager. The methods they developed were described in *The Control of Rats and Mice,* a book published in 1954, and they are still applied all over the world.

The Bureau of Animal Population was headed by Charles Elton (1900–91), a zoologist who believed animals were best studied living wild, in their natural surroundings. This attitude took him away from the emphasis on comparative anatomy that dominated zoology in his student days and toward ecology. Elton became the most influential animal ecologist in Britain. Naturalists had been observing animals in their natural surroundings for centuries, of course, but Elton conducted and taught studies that involved measuring, documenting behavioral details, and performing experiments. At the same time as Arthur Tansley was transforming plant ecology into a rigorous scientific discipline, Charles Elton was doing the same for animal ecology.

Elton considered Alexander von Humboldt as perhaps the first ecologist (*see* "Alexander von Humboldt and Aimé Bonpland, Exploring South America" on pages 79–84) because he wrote about the natural world as a whole and sought to unravel the complex interrelationships governing the fate of plants and animals. His strongest intellectual influence, however, was Victor E. Shelford (*see* "Victor E. Shelford and Animal Communities" on pages 152–153) and his 1913 book describing his investigation of the animal communities around Chicago.

In 1921 the biologist Julian Huxley recruited Elton as an assistant on a field trip to Spitzbergen, in the Norwegian Arctic. Elton surveyed the ecology of the animals living there, using Shelford's methods, and he visited Spitzbergen again in 1923, 1924, and 1930. His experience in the Arctic led the Hudson's Bay Company to offer him a consultancy investigating the long-term fluctuations in fur-bearing animals in northern Canada, using records from trappers going back to 1736. Elton worked for the company from 1925 to 1931. In 1932 he established the Bureau of Animal Population at Oxford University, which quickly attracted scientists from all over the world and acquired an international reputation for scientific excellence. Also in 1932 Elton helped persuade the British Ecological Society to launch the *Journal of Animal Ecology,* which he edited from 1932 to 1935, and later with A. D. Middleton 1936–37, with D. Chitty 1938–50, and with D. Chitty and H. C. Gilson in 1951.

Elton published *Animal Ecology* in 1927. This was a textbook in which he promoted the term *niche,* first used in 1913 by the American zoologist Joseph Grinnell (1877–1939), director of the Museum of Vertebrate Zoology at the University of California, Berkeley. Elton wrote that it is "convenient to have some term to describe the status of an animal in its community, to indicate what it is *doing* and not merely what it looks like, and the term used is 'niche.'" In the same book, Elton introduced the pyramid of numbers, a method for representing graphically the trophic levels in an ecosystem. The illustration on page 172 shows how these work. Two other pyramids were added later (*see* the sidebar on page 173), and these ecological pyramids are sometimes called Eltonian pyramids.

His 1930 book, *Animal Ecology and Evolution,* challenged several widely held ideas, as the following quotation illustrates.

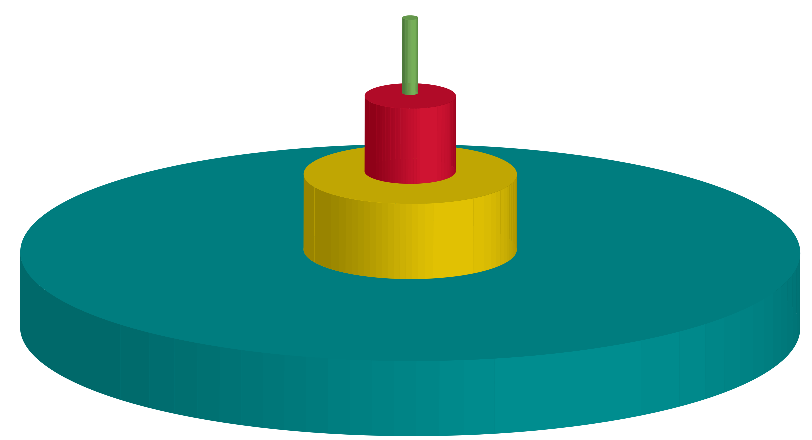
> The "balance of nature" does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or

> less extent, and the variations are usually irregular in period and always irregular in amplitude. Each variation in the numbers of one species causes direct and indirect repercussions on the numbers in others, and since many of the latter are themselves independently varying in numbers, the resultant confusion is remarkable.

He also wrote that in periods of stress it is common for animals to change their habitats, usually by migrating. This led him to conclude that it is not the environment that selects the animal so much as the animal that selects its own environment.

In 1942 Elton published *Voles, Mice and Lemmings,* a book that described and tried to explain the large fluctuations in the populations of these animals in the Arctic. His experiences studying these animals led him to reject the concept of the community and the superorganism. Rather, he looked for the way animals competed for limited food.

Charles Sutherland Elton was born in Withington, Manchester, on March 29, 1900. His father, Oliver Elton, was a literary scholar





An ecological pyramid is a graphic representation of the structure of feeding relationships within an ecosystem. A rectangle represents the producers (green plants). On top of that a second rectangle represents the primary consumers (herbivorous animals). Additional rectangles represent secondary and tertiary consumers. Different pyramids depict the number of organisms (pyramid of numbers), their total mass (pyramid of biomass), and the amount of energy at each level (pyramid of energy).

## ECOLOGICAL PYRAMIDS

In his book *Animal Ecology,* published in 1927, Charles Elton introduced a novel way to depict the relative sizes of the trophic levels within an ecosystem. He represented the producers (usually green plants) by a rectangle and placed further rectangles on top of that rectangle to represent primary consumers (herbivorous animals), secondary consumers (carnivorous animals that feed on herbivores), and tertiary consumers (carnivores that feed on other carnivores). At each level the height of the rectangle remained the same, but its width represented the size of that level. The stacks of rectangles diminish rapidly in size, producing the shape of a stepped pyramid. There are three types of pyramid, each varying somewhat in shape.

The pyramid of numbers represents the number of individual organisms at each level. This is not very useful, however, because it takes no account of the size of the individuals. An area of vegetation can support many more rabbits than it can elephants, for example.

The pyramid of biomass partly avoids this difficulty by representing the mass of dry matter or the energy value of the organisms at each level. It does not avoid the difficulty entirely because small animals have a much higher metabolic rate than larger animals. In extreme cases this produces a greater biomass of consumers than of producers, resulting in an inverted pyramid.

The pyramid of energy is the most useful of the three. It represents the rate of photosynthesis at the producer level and the rate of respiration at each higher level. It does not represent either the numbers or mass of the organisms at each level, and because energy flows through an ecosystem in only one direction—from producer to consumer—the pyramid of energy is never inverted.

Typically, in the pyramids of biomass and energy the primary consumer level is one-tenth the size of the producer level, and each higher consumer level is one-tenth the size of the level below. Thus, if the producer level is given a value of 1,000, that of the primary consumers will be 100, of the secondary consumers 10, and of the tertiary consumers 1. It explains why there are always more herbivores than carnivores, and why there are few carnivores that feed exclusively on other carnivores.

and his mother, Letitia Maynard Elton (born MacColl), a children's author. He was educated at Liverpool College, a private school in Liverpool, and at New College, University of Oxford, where he graduated in zoology in 1922. He remained at Oxford for the rest of his academic career. In 1936 he was appointed lecturer in animal ecology and elected a senior research fellow of Corpus Christi College. He helped found the Nature Conservancy in 1949. He was elected a fellow of the Royal Society in 1953 and received the society's Darwin Medal in 1970. Elton was made an honorary member of the New York

Zoological Society in 1931, and in 1961 he was made a life member and eminent ecologist of the Ecological Society of America. Charles Elton died in Oxford on May 1, 1991.

## RONALD AYLMER FISHER AND THE UNION OF EVOLUTION AND ECOLOGY

A stained-glass window in the dining hall of Gonville and Caius College, University of Cambridge, depicts a Latin square. A Latin square is a table with the same number of rows as there are columns (making it square), filled with numbers or other symbols such that each number or symbol appears once and once only in each row and once and once only in each column. The following illustration shows a very simple Latin square made from four numbers:

1 2 3 4
2 1 4 3
3 4 1 2
4 3 2 1

The Latin square in the Cambridge window uses colors rather than numbers, and there are seven of them. Latin squares possess properties that interest mathematicians, and Sudoku puzzles are a variety of them. They are rarely used simply to honor a mathematician, but that is the purpose of the stained-glass window at Caius College. It honors the English statistician, geneticist, and evolutionary biologist R. A. Fisher (1890–1962).

Fisher laid the foundations for much of modern statistics and in particular the application of statistical methods to biological data. He demonstrated that Mendel's laws (*see* sidebar on page 175) must inevitably produce the results that are observed and also that Mendelian inheritance can explain Darwinian evolution by natural selection. This made him one of the founders of the modern evolutionary synthesis that unites the theories of evolution by natural selection and inheritance (*see* "Henry Allan Gleason and the Individualistic Concept" on pages 150–152). His work on the statistics of inheritance led to studies of *population genetics*—the study of heritable variations among members of a population. This involves estimating the frequency of particular genes in the population and the effects of natural selection, mutation, and the movement of individual organisms into and out of the population. Together with the American geneticist Sewall Wright (1889–1988) and the British geneticist J. B. S. Haldane (1892–1964), Fisher is regarded as one of the greatest scientists in this field.

His work on population genetics led Fisher to investigate the genetics of the way populations of organisms relate to their environment. This is called "ecological genetics," and Fisher formed a long and fruitful collaboration with the English biologist E. B. Ford (1901–88). They showed that natural selection was a more powerful force than many had previously supposed.

Ronald Aylmer Fisher was born in East Finchley, London, on February 17, 1890. His father, George Fisher, was a partner in a successful firm of art auctioneers, and his mother, Katie Heath, was the daughter of a solicitor. Katie died in 1904, when Ronald was 14, and 18 months later George lost all his money in business dealings that failed. It was

## MENDEL'S LAWS

On March 8, 1865, the Augustinian monk Gregor Mendel (1822–84) from the monastery at Brünn, Austria (now Brno, Czech Republic) presented a paper to the local Naturförscher Verein (natural research society) describing experiments he had conducted over several years cross-breeding peas, and the results he had found. Mendel had grown the peas in the monastery garden, commencing his experiments in 1856 using peas with several distinctive traits. His results resolved themselves into what are now known as Mendel's two laws or principles of inheritance.

Expressed in modern language, Mendel's first law states that when a pair of genes separates during meiosis, each resulting egg or sperm cell has an equal chance of receiving either member of the pair. This is called the law of segregation.

Mendel's second law states that when pairs of genes separate during meiosis each pair does so independently of all the other pairs. This is the law of independent assortment. (The second law was at first thought to apply universally, but it is now known to apply only to pairs of genes that are not linked together or that are linked only loosely.)

Genes had not yet been discovered when Mendel performed his experiments, and he described not genes but "factors" within pairs of characters. Mendel's paper, published in an obscure journal, aroused little attention until 1900, when Carl Erich Correns (1864–1933) in Germany, Hugo de Vries (1848–1935) in the Netherlands, and Erich Tschermak von Seysenegg (1871–1962) in Austria, all discovered it independently in the course of searching the scientific literature in connection with their own researches.

at this time, in 1904, that Ronald entered Harrow School, a private boys' school, where he won the Neeld Medal, a major mathematics prize, at the age of 16. His eyesight was extremely poor, and he was taught mathematics orally. It is said that this encouraged him to envisage problems geometrically rather than algebraically. While at Harrow, Fisher also acquired a strong interest in biology. In 1909 he won a scholarship to Gonville and Caius College, Cambridge, graduating with distinction in 1912. He remained at Cambridge, but after leaving in 1913, he needed to earn a living and so moved to Canada, where he spent several months working on a farm. Then he returned to London and found employment as a statistician at the Mercantile and General Investment Company.

Fisher was very patriotic and had belonged to the Officers' Training Corps at Cambridge, so when it became obvious that World War I was soon to begin, he tried to enlist but was rejected because of his eyesight. Instead, he became a mathematics and physics teacher at several schools from 1915 to 1919. A college friend from his Cambridge days introduced him to her sister, Ruth Eileen Gratton Guinness. Ronald and Eileen were married in 1917, shortly after Ruth Eileen's 17th birthday. They had two sons and seven daughters. One daughter died in infancy, and their eldest son, George, lost his life as a pilot in World War II. Using skills he had learned on the Canadian farm and with the help of the two sisters, Fisher established a small farm on the estate belonging to the school where he was teaching, growing vegetables and raising livestock, and he and his wife were able to feed themselves.

In 1919 Fisher was offered the post of statistician at Rothamsted Experimental Station, and he gave up teaching, not least to pursue his interest in farming. Founded in 1843, Rothamsted Experimental Station (now called Rothamsted Research), near Harpenden a few miles north of London, is one of the oldest agricultural research stations in the world. Fisher studied the data on crops gathered over many years, publishing his findings in a series of reports called *Studies in Crop Variation.* He also studied and improved the design of experiments and made many valuable contributions to the statistical interpretation of experimental data. At the same time, he conducted breeding experiments of his own on mice, snails, and chickens. This led to his book *The Genetical Theory of Natural Selection,* published in 1930.

In 1933 Fisher was appointed Galton Professor of Eugenics at University College, London, but on the outbreak of war in 1939 he returned to Rothamsted. He remained there until 1943, when he became Arthur Balfour Professor of Genetics at the University of Cambridge. By this time, his marriage had ended. Fisher retired in 1957, but continued working for two more years while the university sought his replacement. He then moved to the University of Adelaide, Australia, as a senior research fellow at the CSIRO (Commonwealth Scientific and Industrial Research Organization). He died in Adelaide on July 29, 1962.

Fisher received many honors. He was elected a fellow of the Royal Society in 1929. In 1938 he was awarded the society's Royal Medal and in 1955 its Copley Medal. He received the Guy Medal in Gold of the Royal Statistical Society in 1946. He was knighted in 1952.

10

# The Rise of Sociobiology

Carnivores hunt herbivores, but herbivores have several ways to avoid being eaten. They have acute senses that warn them of danger in time for them to escape, and they may be able to run, fly, or swim faster than their pursuer. They may be so well camouflaged that they are difficult to detect. Some, such as monarch butterflies (*Danaus plexippus*), are poisonous to any predator trying to devour them, while others are harmless and edible, but closely resemble a poisonous species, so that predators learn to avoid any animal with that appearance. It is easy to see how these and many other protective features are acquired through the process of evolution by natural selection.

There are other ways to evade capture that are more difficult to explain. Many species of fish swim in schools. If a predator threatens, the school forms a tight sphere. It comprises thousands of fish, but the predator finds the sight confusing and is unable to select an individual target. Many species of birds form flocks that are very similar to schools of fish. Grazing animals usually live in herds or flocks. While an animal is bending down to feed, it is unable to maintain a wary eye on its surroundings, but within a herd there are always some individuals with their heads raised, alert to danger, and should they detect an approaching predator, they will start to run and the rest of the group will follow.

How does behavior of this kind evolve? Parents in many species care for their offspring until the young are able to fend for themselves. This behavior requires one or both parents to pass to their young food they could have consumed themselves, to expend energy constructing a secure nest, and to risk their own safety to protect young that are incapable of fleeing or defending themselves. How did this behavior evolve? There are more extreme examples. Among social insects such as ants and many species of bees and wasps only the queen lays eggs, and the rest of the colony consists of females that are incapable of reproduction and devote their entire existence to the construction, repair, and protection of the nest or hive and the raising of the larvae. Why do they give up any chance of reproducing?

Thomas Malthus believed that all animals produce as many young as they are capable of doing and that most offspring die young from starvation, disease, or predation, so the size of a population is maintained at the highest level the environment can support (*see* "Population and Resources" on pages 96–101). Some animals do behave in this way, but others restrict their reproduction. Why is this?

These questions concern the way animals adapt to their environments. They relate to both evolution and ecology, and by the early decades of the 20th century biologists were seeking answers. To assist them they had the powerful statistical methods being developed by R. A. Fisher and others (*see* "Ronald Aylmer Fisher and the Union of Evolution and Ecology" on pages 174–177). One result of this inquiry was the emergence of a branch of biology that drew on studies of animal behavior, anthropology, and population genetics as well as evolution and ecology. This new science was introduced in 1975 by E. O. Wilson (1929– ). He called it sociobiology. This chapter briefly reviews the development of sociobiology.

## WILLIAM D. HAMILTON AND THE EVOLUTION OF BEHAVIOR

*Through the Looking-Glass, and What Alice Found There,* by Lewis Carroll, is one of the best loved of all children's stories. In 1973 the American evolutionary biologist Leigh M. Van Valen (1935– ) used the following episode in the book to illustrate the evolutionary principle that the evolution of a species consists to a large extent of keeping up with environmental changes.

> Well, in our country," said Alice, still panting a little, "you'd generally get to somewhere else—if you ran very fast for a long time, as we've been doing." "A slow sort of country!" said the Queen. "Now, *here,* you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that.

This principle is called the Red Queen hypothesis, and it suggests that species are constantly evolving toward perfect adaptation to their environments, but never quite achieving it. For Van Valen it represented the way sexual reproduction had evolved as a means of protecting species from disease-causing parasites. It happens because sexual reproduction involves rearranging combinations of genes, so each generation presents parasites with slightly altered cell structures, affording a measure of protection. The parasite evolves ways around the host defenses, and the host evolves new defenses in an endless race.

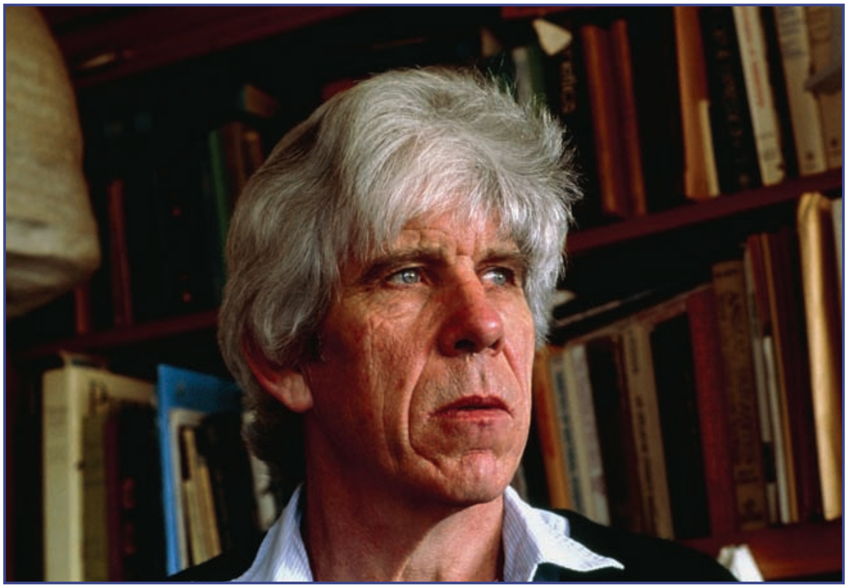
William D. Hamilton (1936–2000) strongly supported this aspect of the Red Queen hypothesis. He possessed a profound understanding of evolution. While a student, he read R. A. Fisher's book *The Genetical Theory of Natural Selection,* published in 1930, in which Fisher explained natural selection mathematically. Hamilton was deeply influenced by the book, but at the time biologists, including Hamilton's teachers, regarded Fisher purely as a statistician and not competent to comment on evolutionary matters. When Fisher's book was reprinted in 1999, Hamilton wrote on the dust jacket that he blamed the book for the fact that he received only a second-class degree, and then asked: "by the time of my ultimate graduation, will I have understood all that is true in this book, and will I get a first?"

Other biologists had noted that an organism could enhance its own evolutionary fitness by assisting close relatives with which it shared genes. The English biologist J. B. S. Haldane (1892–1964) is reputed to have said that he would lay down his life for more than two brothers or sisters, eight cousins, 32 second cousins, and so forth as the relationship became more distant. Hamilton developed this into a general rule, stating that it is worth helping a relative if in doing so the performer reduces its fitness by less than the amount by which the recipient gains fitness multiplied by the degree of relationship (in which an identical twin = 1; a sibling = 0.5; a grandparent or grandchild = 0.25; a cousin = 0.125, etc.).

This led Hamilton to write a paper entitled "The Genetical Evolution of Social Behavior," which appeared in 1964 in two installments in the *Journal of Theoretical Biology.* At the time Hamilton was still a Ph.D. student. The paper aroused little interest, but as the years passed, its importance became more evident, although Hamilton's rule has still not been proved. Hamilton had directed scientific attention to the evolution of social behavior and had demonstrated that the evolutionary fitness of an organism should take account of the reproductive success of all of its kin, as well as of its own success. This is called *inclusive fitness,* and it showed why such *eusocial*—highly social—societies as those of termites, ants, and honeybees—as well as naked mole rats (*Heterocephalus glaber*), the only eusocial mammal—were successful and stable.

William Douglas Hamilton was born in Cairo, Egypt, on August 1, 1936, the second of six children. His father was an engineer, born in New Zealand, and his mother was a physician. The family returned to England and settled in Kent, but on the outbreak of World War II William was evacuated to Edinburgh. He returned to Kent to attend Tonbridge School, but when he was 12 he suffered serious injuries playing with explosives that his father had been using to make hand grenades for the Home Guard—the defense force composed of volunteers who were unsuitable for ordinary military service, most because they were too old. His mother saved his life, but it took six months for him to recover, and his body remained badly scarred. Hamilton passed the entrance examinations for Cambridge University, then spent time traveling in France before enlisting for his compulsory two years of military service.

After graduating from St. John's College, Cambridge, Hamilton studied human demographics at the London School of Economics (LSE) for a master's degree and went on to earn a Ph.D. from LSE and University College London (both institutions are part of the University of London) in 1968. From 1964 to 1977, Hamilton was a lecturer at Imperial College (also part of London University). In 1978 he became professor of evolutionary biology at the University of Michigan, Ann Arbor, and in the same year he was elected a foreign honorary member of the American Academy of Arts and Sciences. He was elected a fellow of the Royal Society in 1980, and in 1984 Sir



William D. Hamilton (1936–2000) was the Royal Society Research Professor at the University of Oxford. He was regarded as one of the greatest evolutionary biologists of the 20th century. This photograph was taken in 1996. *(James King-Holmes/Science Photo Library)*

Richard Southwood (1931–2005), Linacre Professor of Zoology at the University of Oxford, invited him to join the zoology department at Oxford as the Royal Society Research Professor. Hamilton accepted the post and remained there until his death. The photograph above shows Hamilton at the age of 60.

During the 1980s Hamilton became convinced that HIV (human immunodeficiency virus) originated in oral polio vaccines that had been prepared in chimpanzee tissue cultures and administered experimentally to up to 1 million Africans between 1957 and 1960. Seeking evidence for this, he traveled to the Democratic Republic of the Congo to collect chimpanzee feces, from which he hoped to extract a virus related to the human virus. While there he contracted malaria. He returned to London, but died from a cerebral hemorrhage six weeks later, on March 7, 2000. In the obituary he wrote for *The Independent* newspaper, Richard Dawkins described Hamilton as “a good candidate for the title of most distinguished Darwinian since Darwin.”

## EDWARD O. WILSON AND SOCIOBIOLOGY

W. D. Hamilton had shown that some animal behavior is inherited and that behavior can evolve. His work led others to investigate a wide variety of behaviors and especially social behaviors. It is not difficult to see that certain patterns of behavior consist of sequences of actions in which what one player does stimulates the appropriate response in the other player. The courtship rituals of many birds and fishes are of this kind, as is the ritualized aggression between males contesting for territory or mates that allows the contestants to judge which of them is the stronger without actually inflicting injuries.

There are many examples of animal behaviors that can be explained in this way, but certain social behaviors are more difficult to explain. A member of a flock of birds that utters a warning cry on seeing a predator draws attention to itself when it might be safer to escape or hide. So why does it do this? It is common for human couples to adopt orphaned children and raise them as though they were their own. Perhaps adoption happens because most people take pity on orphans out of fellow feeling for others. That may be so, but adoption is not confined to humans. Many bird and mammal species adopt orphans, and not only are the adoptees sometimes unrelated to the adopters, occasionally they are not even of the same species. In most cases animals adopt because they have recently lost an offspring or they are unable to reproduce. But is this the whole explanation for every case?

In 1931 the American ecologist Warder Clyde Allee (1885–1955) was among the first to explore these questions in his book *Animal Aggregations: A Study in General Sociology.* Allee was professor of zoology at the University of Chicago and spent his summers working at the Marine Biology Laboratory, Woods Hole, Massachusetts, where he studied crustaceans and other animals that gathered in large groups. He concluded from his studies that among certain animals the benefits of social cooperation outweighed those that individuals could obtain through competing. He developed this idea in his book *The Social Life of Animals,* published in 1938, and in *Principles of Animal Ecology,* published in 1949, which Allee coauthored with Orlando Park, Alfred E. Emerson, Thomas Park, and Karl P. Schmidt.

Edward O. Wilson (1929– ) photographed with a microscope in 1983. Wilson argued that animal behavior, including human behavior, results from evolution, launching a controversial scientific discipline called sociobiology. *(Steve Liss, Time & Life Pictures)*

Other biologists developed the theme of social cooperation, culminating in the 1975 publication of the book *Sociobiology: The New Synthesis* by Edward O. Wilson (1929– ). Wilson argued in his book that natural selection has shaped many social behaviors because they increase the likelihood that those performing them will produce more offspring that grow up to produce more offspring of their own—in other words that the behaviors increase evolutionary fitness. The final chapter in Wilson's book dealt with the evolution of human behavior. This provoked strong reactions that were based on a misunderstanding of what Wilson was saying. The fact that a particular type of behavior is evolutionarily adaptive does not mean it cannot be changed. If the environment changes, then natural selection may favor a different type of behavior, and humans are not compelled to behave in a particular way simply because that is the way they evolved to behave. All Wilson sought to do was to explain the evolutionary significance of different types of behavior in animals, including humans. He simply offered a new way of looking at behavior.

Edward Osborn Wilson was born on June 10, 1929, in Birmingham, Alabama. He spent his childhood in several towns in Alabama and Florida, and in Washington, D.C. He studied biology at the University of Alabama, where he earned his bachelor's and master's degree, spent a year as a graduate student at the University of Tennessee, then moved to Harvard University, where he obtained his Ph.D. in 1955. He joined the Harvard faculty in 1956 and is now Pellegrino University Professor Emeritus and Honorary Curator in Entomology. The photograph above of Wilson was taken in 1983.

Wilson devoted much of his research to the ecology and classification of ants, becoming a world authority on these insects. He and others explored the way ants communicate using chemical signals called *pheromones.* In the early 1960s he collaborated with Robert H. MacArthur in developing the theory of island biogeography (*see*

"Robert H. MacArthur and the Testing of Hypotheses" on pages 153–155). In addition to his research, since the late 1970s Wilson has been actively involved in wildlife conservation and the promotion of research into biodiversity. He and his wife, Irene, live in Lexington, Massachusetts.

11

# Ecology and Environmentalism

At various periods throughout history, people have expressed concern about the condition of the environment. Traffic congestion in cities is nothing new. One-way streets were introduced to reduce congestion in Rome during the rule of Julius Caesar (100 B.C.E.–44 B.C.E.), and all vehicles except for those belonging to high-ranking citizens and public officials were banned from the city center. In 1812 a London court convicted a driver of permitting a stagecoach to remain for three-quarters of an hour, twice a day, in the street near Charing Cross train station "to the annoyance of the King's subjects."

Smoke pollution has been a problem probably ever since people have lived in cities and burned fuel to heat their homes, cook their food, and power their manufactures. The English King Edward I (1239–1307) attempted to reduce the nuisance caused by smoke in London with a law in 1273, and in 1306, with the situation deteriorating, he banned the use of coal in London. Queen Eleanor (1223–91) fled from Nottingham Castle in 1257 because the smoke was so bad that she feared for her life. In 1578 Elizabeth I (1533–1603) refused to enter London because the smoke was so bad. The author and diarist John Evelyn (1620–1706), in *A Character of England,* published in 1659, described London pollution in the following words:

> . . . this pestilential smoke which corrodes the very iron, and spoils all the moveables, leaving a soot on all things that it lights; and so

> fatally seizing on the lungs of the inhabitants, that cough and consumption spare no man.

In the Middle Ages statutes were passed in England for the upkeep of the River Thames, including its banks and the fish and their young within it. The lord mayor and aldermen of London, who were charged with upholding these laws, were entrusted with the river's "conservacie." This is possibly the first use of the word *conservation.* Long before the word *conservation* was coined, around 300 B.C.E. the Chinese philosopher Mencius wrote about the adverse effects of overgrazing and deforestation due to excessive demand for timber.

Environmental concern is far from being a recent phenomenon. The present popular environmental movement began in the 1960s and reached its first peak of influence in the early 1970s. This chapter describes its origin.

## RACHEL CARSON AND *SILENT SPRING*

It is not often that a book alters the way millions of people think about the way they live and the environment in which they live, but just such a book was published in 1962. It was called *Silent Spring,* and it has not been out of print since. Its publication was well prepared. Excerpts from the book appeared as articles in *The New Yorker* magazine prior to its becoming available in bookstores. *Silent Spring* criticized the careless and excessive use of agricultural pesticides, and it aroused strong and well-publicized opposition from pesticide manufacturers. The fame the book achieved led to the emergence of the modern environmental movement, first in the United States and Britain, and soon afterward throughout western Europe and Australasia, and eventually most of the world.

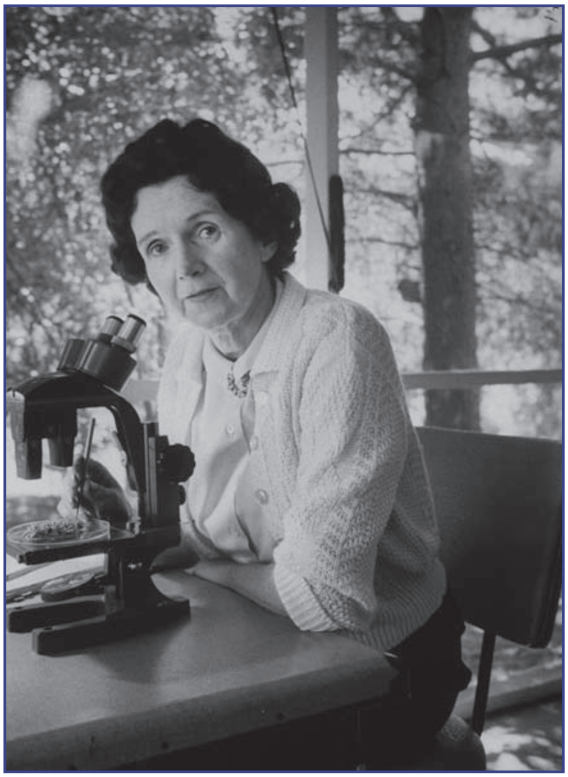
The book's author was Rachel Carson (1907–64), an American biologist who was already a very successful author. Trained as a marine biologist, her earlier books included *Under the Sea-Wind* (1941), *The Sea Around Us* (1951), and *The Edge of the Sea* (1955). The first chapter of *Silent Spring* was entitled "A Fable for Tomorrow," and it set the tone for the whole book. It described a fictitious American town where "mysterious maladies swept flocks of chickens; the cattle and sheep sickened and died. . . . The farmers spoke of much illness among their families." Then one spring the town fell silent because all the songbirds had died from pesticide poisoning. Carson did not claim that all of these misfortunes had struck any single town, but she said "every one of these disasters has actually happened somewhere, and many real communities have already suffered a substantial number of them."

Carson was not opposed to the use of pesticides. She recognized the contribution their use had made to increases in agricultural output. Her fear was that they were being used indiscriminately and excessively, without proper regard to their side effects. The chemicals that concerned her were organochlorine insecticides, the first generation of modern pesticides. These were chemically stable, which meant that once they had been applied they remained active for a considerable time. That was one of their advantages, but it concealed their principal disadvantage, which was that their persistence made it possible for them to accumulate along food chains. Earthworms absorbed small amounts, which were retained in their bodies. Small birds ate the worms, accumulating in their bodies the insecticide contained in each of the worms they ate. A bird of prey fed on smaller birds, accumulating all of the insecticide from their bodies. Eventually, birds of prey, the top predators, would have a bodily concentration high enough to produce adverse effects, the most common of which was failure to reproduce. Also, these poisons were fairly indiscriminate. Designed to poison insect pests, they also poisoned many other insects, including some of the natural predators that otherwise helped limit the size of pest populations.

It was a powerful indictment that spoke clearly to a generation of young people who had already marched in protest against the atmospheric testing of nuclear weapons and against the war in Vietnam. Nuclear war might happen or it might not, but environmental poisoning by pesticides, said Carson, was already happening. The organic farming movement flourished as people grew to fear that their food also contained these poisons. Within a few years, concern about environmental pollution merged with fears that the industrialized nations were in imminent danger of running out of mineral resources and that the rate of food production could not keep up with the rate of human population growth, threatening countless millions of people with starvation.

*Silent Spring* concentrated on the effects of organochlorine insecticides, the best known of which was DDT (*pp′*dichlorodiphenyltrichloroethane). The book conveyed so powerful a message that many nonscientists supposed Carson was the first person to alert the public to the risks. This was not so. DDT was first patented in 1943, and within a few years entomologists were warning of its potential dangers. One of the earliest warnings was given on February 15, 1945, at a London meeting of the Royal Society of Tropical Medicine, by Kenneth Mellanby (1908–93), an entomologist who later became one of the world's leading authorities on environmental pollution. Mellanby said that while DDT "was probably the greatest advance in insect control that had ever been made . . . DDT was clearly no panacea, which could be broadcast indiscriminately to kill off all noxious pests." Several American scientists made similar comments, and it is likely that biologists would soon be calling for strict controls on the use of DDT and related compounds.

Public pressure demanded more. The most hazardous organochlorines were banned outright, and before long DDT joined them, despite being relatively harmless. Not all the consequences were benign. DDT was, and is still, the most effective insecticide for use against the mosquitoes that transmit malaria, but in 1964 spraying of DDT for this purpose was halted in Sri Lanka. In 1948 there had been 2.8 million cases of malaria reported in Sri Lanka, but by 1963 the number had fallen to 17, thanks to the use of DDT. Following the ban, by 1969 the number had risen to 2.5 million. When the use of DDT ended, a less persistent but more toxic insecticide, parathion, was substituted. None of the operatives spraying DDT had ever been harmed by it, but many deaths occurred among those spraying parathion. Today the use of DDT is permitted for mosquito control in regions where malaria is prevalent.



Rachel Carson (1907–64) was the American biologist and author whose book *Silent Spring* warned of the risks of excessive use of persistent pesticides. This photograph was taken in 1962. *(Time & Life Pictures)*

Rachel Louise Carson was born on May 27, 1907, in Springdale, Pennsylvania. She began writing as a child and later entered Pennsylvania College for Women to study English, with the intention of making writing her career. She switched to biology, however, graduating in 1929 and obtaining her master's degree in genetics in 1932 from Johns Hopkins University, while also studying zoology at the University of Maryland. She had joined the faculty of the University of Maryland in 1931 and taught there until 1934, and from 1929 to 1936 she also taught at the Johns Hopkins summer school. Carson continued her postgraduate studies at the Marine Biological Laboratory, Woods Hole, Massachusetts.

In 1936 Carson obtained a post as an aquatic biologist with what was then called the U.S. Bureau of Fisheries (it became the U.S. Fish and Wildlife Service in 1940). She remained there until 1952, in the last years as editor in chief of the service's publications. The photograph on page 189 of Rachel Carson, taken in 1962, shows her with a microscope and petri dish. She died from cancer at Silver Spring, Maryland, on April 14, 1964.

## THE RISE OF THE ENVIRONMENTALIST MOVEMENT

*Silent Spring* drew attention to an environmental problem by dramatizing and exaggerating it, and soon other scientists were using the same technique. In 1968 Garrett Hardin reworked an 1833 paper as "The Tragedy of the Commons," which was published in *Science* (*see* "Public or Private? 'The Tragedy of the Commons'" on pages 40–43), and in the same year Paul R. Ehrlich, an entomologist at Stanford University, published *The Population Bomb.* Ehrlich produced alarming figures to show that the human population was doubling approximately every 37 years, and he pointed out that if that rate of increase were to continue, in 900 years the Earth's population would amount to 60 million billion persons ($60 \times 10^{15}$), which he calculated worked out at 100 persons for every square yard of the Earth's surface (about 120 per $m^2$). Ehrlich urged an end to population growth, especially in the industrialized countries because of their disproportionate consumption of resources.

Over the following few years, hundreds of books appeared in the United States and Britain repeating the warnings from Carson, Hardin, Ehrlich, and others. Some of the authors were scientists, but most were not. A few of the books were thoughtful and well written, but most were not. Among the scientists, however, there were some who had used published data to calculate that modern industries were consuming resources at a rate that could not be sustained.

A few scholars tried to demonstrate that humanity was not doomed, but their lone voices were overwhelmed by the sheer volume of books expressing pessimistic views. Pessimism about the future became the received wisdom, and it reached to the highest levels in industry and government. In April 1968, Aurelio Peccei, an Italian industrial manager, brought together 30 scientists, educators, economists, humanists, industrialists, and civil servants from 10 countries. They met at the Accademia dei Lincei in Rome, and from that meeting grew The Club of Rome, an informal association, eventually with approximately 70 members from 25 countries, which set itself the task of examining the complex of problems facing the world.

The Club of Rome's first undertaking was called the Project on the Predicament of Mankind, which began in 1970 with a study by a team at the Massachusetts Institute of Technology (MIT), led by Professor Jay Forrester. Forrester and his colleagues studied the theory of systems, and they tackled the Club of Rome project by constructing one of the very earliest computer models of the world. Their model followed the interaction of five factors that the team considered fundamental: population, agricultural production, natural resources, industrial production, and pollution. The result of their modeling was published in 1972 as a book by Donella H. Meadows and others entitled *The Limits to Growth.* The first part of the conclusion was as follows:

> If the present growth trends in world population, industrialization, pollution, food production, and resource depletion continue unchanged, the limits to growth on this planet will be reached sometime within the next one hundred years. The most probable result will be a rather sudden and uncontrollable decline in both population and industrial capacity.

This catastrophic scenario could be avoided, the report said, if society altered its behavior to bring its material demands into equilibrium with the capacity of the environment to supply them. The recommendation referred to this as "ecological and economic stability." The use of the word *ecological* marks a slight shift in meaning, for this was essentially an economic and political study that was very different from the biological study of communities and ecosystems. In subsequent years, this difference widened, and today, although environmentalists, not to mention manufacturers seeking to attract environmentally concerned customers for their products, often use such words as *ecology* and *ecosystem,* modern environmentalism is a philosophical and political belief system only loosely based on the science of ecology.

In Britain a group of writers saw an early copy of the *Limits to Growth* results and used it as the base from which they constructed their own program. This team, of Edward Goldsmith, Robert Allen, Michael Allaby, John Davoll, and Sam Lawrence, wrote a document that filled the January 1972 issue of *The Ecologist* magazine. They called their paper "A Blueprint for Survival." It appeared later in book form and was translated into many languages. At the time of its first publication, the Blueprint attracted widespread media attention, not least because a number of eminent scientists had endorsed it.

The string of books followed by *The Limits to Growth* and "A Blueprint for Survival" firmly established the idea that modern industrial society will fail, most probably in the very near future. This remains the underlying belief of the environmentalist movement. Friends of the Earth was formed in 1970 by David Brower, formerly executive director of the Sierra Club. A British branch opened in 1971, and within a few years there were branches in most countries. Greenpeace began in 1977, initially with campaigns to oppose whaling, marine pollution, and nuclear power. The World Wide Fund for Nature is now one of the leading environmentalist organizations, but it began as a primarily fund-raising body linked to the International Union for Conservation and Resources (World Conservation Union), devoted to the conservation of wildlife. All of these bodies, and others, attack what they see as the unsustainability of modern society.

## THE STOCKHOLM CONFERENCE AND THE UNITED NATIONS ENVIRONMENT PROGRAMME

Rising environmental concern culminated with the involvement of the United Nations. Around 1970 the Swedish government asked the United Nations to consider the problem, and UN Secretary-General U Thant invited Maurice F. Strong (1929–    ) to organize a major conference on the topic and to be secretary-general of what would officially be called the UN Conference on the Human Environment; informally it was known as the Stockholm Conference.

Maurice Strong is a Canadian businessman and diplomat. Born in Manitoba during the Great Depression, Strong worked for the Hudson's Bay Company in the far north, as a security officer at the United Nations in New York, and later in the petroleum industry. His experience on corporate boards allowed him to speak publicly about Canadian foreign policy—he believed Canada should do more to help developing countries. This attracted the attention of Prime Minister Lester B. Pearson (1897–1972), who made Strong a deputy minister in the External Aid Office, which Strong expanded into the Canadian International Development Agency (CIDA). As the head of CIDA, Strong was able to return to the United Nations as a member of the Canadian delegation. At the same time, since his youth Strong had had a keen interest in the natural environment and supported the conservation and environmentalist movements.

In 1971, as part of the preparations for the forthcoming U.N. conference, Strong commissioned a report that would outline the background to the matters the conference would debate. That report was written by Barbara Ward (1914–81), a British economist with a special interest in developing countries and environmental matters, and the French–American biologist René Dubos (1901–82). Ward and Dubos consulted 152 expert advisers, drawn from many countries, and blended their views into a coherent summary. Their report was published as a book entitled *Only One Earth: The Care and Maintenance of a Small Planet.* The following passage from their introduction explains how the authors defined the purpose of the conference.

> The statesmen who planned the U.N. Conference on the Human Environment . . . were naturally preoccupied with the shortage of food and amenities, the depletion of natural resources, the accumulation of environmental pollutants, the increase in the world population and also the threat to certain natural values which transcend bodily needs. They realized in addition that all these problems have acquired an element of extreme urgency from the fact that mankind has now spread over the whole surface of the globe. By the year 1985, according to recent estimates, all land surfaces will have been occupied and utilized by man, except for those areas which are so cold or at such high altitudes that they are incompatible with continued human habitation or exploitation.

The conference took place in Stockholm, Sweden, from June 5 to June 16, 1972. Representatives attended from 113 countries, 19 intergovernmental agencies, and more than 400 nongovernmental organizations (NGOs). It was the first U.N. conference NGOs were allowed to attend as observers, and it was the first major conference in which the People's Republic of China played an active part. As the conference proceeded, it became evident that many developing countries suspected that the environmental concern expressed by the rich countries had the ulterior motive of restricting their economic development. On their insistence, the final agreement made clear the general opposition to all forms of colonialism and discrimination. By the end of the conference, the delegates had agreed on a long declaration that began with a seven-point proclamation, commencing with the following:

1. Man is both creature and moulder of his environment, which gives him physical sustenance and affords him the opportunity for intellectual, moral, social and spiritual growth. In the long and tortuous evolution of the human race on this planet a stage has been reached when, through the rapid acceleration of science and technology, man has acquired the power to transform his environment in countless ways and on an unprecedented scale. Both aspects of man's environment, the natural and the man-made, are essential to his well-being and to the enjoyment of basic human rights including the right to life itself.
2. The protection and improvement of the human environment is a major issue which affects the well-being of peoples and economic development throughout the world; it is an urgent desire of the peoples of the whole world and the duty of all Governments.

The declaration also stated 20 principles, beginning with the following:

> Man has the fundamental right to freedom, equality and adequate conditions of life, in an environment of a quality that permits a life of dignity and well-being, and he bears a solemn responsibility to protect and improve the environment for present and future generations. In this respect, policies promoting or perpetuating apartheid, racial

> segregation, discrimination, colonial and other forms of oppression and foreign domination stand condemned and must be eliminated.

Following the conference, the declaration and an agenda for action were presented to and adopted by the General Assembly. One of the recommendations from the conference was that the United Nations should establish a body to coordinate the environmental activities of national governments. This recommendation was implemented with the formation of the United Nations Environment Programme (UNEP), with headquarters in Nairobi, Kenya.

UNEP addresses environmental issues at regional and global levels. It coordinates the environmental activities of its member governments, and when it becomes aware of new environmental issues, it brings these to the attention of its members. Its mission statement states the following:

> To provide leadership and encourage partnership in caring for the environment by inspiring, informing, and enabling nations and peoples to improve their quality of life without compromising that of future generations.

The Stockholm Conference was followed 20 years later by the U.N. Conference on Environment and Development, known informally at the Rio Summit or the Earth Summit. Once again the secretary-general was Maurice F. Strong, and this time the conference was held in Rio de Janeiro, Brazil, from June 3 to June 14, 1992. It was a bigger affair than the Stockholm Conference, attended by representatives of 172 governments, and heads of government or heads of state represented 108 of those governments. In addition, there were approximately 2,400 representatives from NGOs.

*Our Common Future,* the book that supplied the background to the conference, was prepared by the World Commission on Environment and Development, chaired by Gro Harlem Brundtland, a former prime minister of Norway. The World Commission took a much more optimistic view than that of Ward and Dubos, as the following excerpt shows.

> The Commission believes that people can build a future that is more prosperous, more just, and more secure. Our report, *Our Common*

> *Future,* is not a prediction of ever increasing environmental decay, poverty, and hardship in an ever more polluted world among ever decreasing resources. We see instead the possibility for a new era of economic growth, one that must be based on policies that sustain and expand the environmental resource base. And we believe such growth to be absolutely essential to relieve the great poverty that is deepening in much of the developing world.

This was the report that emphasized the concept of sustainable development, defined by the commission as development that meets the needs of the present without compromising the ability of future generations to meet their own needs. The Rio Summit produced a plan for action, called Agenda 21, a formal declaration, a statement of forest principles, and two conventions: the U.N. Framework Convention on Climate Change and the U.N. Convention on Biological Diversity. A convention is an agreement that can be presented to bodies capable of using it as a basis for legislation.

## ENVIRONMENTAL PROTECTION AND REDUCING POLLUTION

Long before the United Nations began to coordinate the activities of its member governments through UNEP, most industrialized countries had taken significant steps to reduce the damage that was being done to their air and water. Acid rain, one of the forms of air pollution that caused great concern around the time of the Stockholm Conference, was first noted in 1852, when Robert Angus Smith (1817–84), a Scottish chemist, delivered a paper entitled "On the Air and Rain of Manchester" to the Manchester Literary and Philosophical Society. Smith had observed that rain falling downwind from Manchester—then one of Britain's most important manufacturing cities—was more acid than rain falling elsewhere and that its acidity decreased with increasing distance from the Manchester factories. In 1872 Smith took his finding to a wider audience with the publication of his book *Air and Rain: The Beginnings of a Chemical Climatology.*

In 1863 the British government established an official agency with the task of monitoring industrial air pollution and bringing it under control. At the time, the manufacture of washing soda was the most polluting industry, so the agency was called The Alkali Inspectorate, and it was established under the Alkali Act 1863. Washing soda (sodium carbonate, $Na_2CO_3$) was used for household cleaning, but most was used by the glass, soap, dyestuffs, and paper industries. It had wide use, and the by-product of its manufacture was an exceedingly alkaline sludge that was being dumped on open ground, where it poisoned all plants and animals exposed to it.

London was once notorious for its "pea souper" fogs. They darkened the sky, so streetlights were lit in the middle of the day, traffic moved at a crawl—if it moved at all—and pedestrians walked with one hand touching the wall to guide them. These were the fogs made by mixing ordinary fog with smoke from millions of coal fires that in 1911 a member of the Coal Smoke Abatement Society proposed calling "smog." London pea soupers have been immortalized in movies, where they provided concealment for criminals, but they were not confined to London. Throughout most of the 19th century and the first half of the 20th, fogs of this type occurred in most European and North American industrial cities. They began to disappear when lawmakers introduced legislation to curtail the use of coal in domestic open fires. They are now a thing of the past, but in their day their soot soiled clothes, smeared windows, and aggravated respiratory complaints. Smog could kill, and sometimes it did.

Many industrial processes use water. Factories used to take their water from a river and discharge their effluent into the same river, downstream from the intake so they could import clean water and export contaminated water. The time came when so many factories lined the banks of all the major rivers in industrial countries that there no longer was any clean water for them—and very few organisms were able to live in the rivers. Some rivers were so polluted that occasionally they caught fire. Governments legislated to limit what factories were permitted to discharge and how much. Today those rivers are much cleaner, and fish have returned to them.

Industries also contaminated land with oil and heavy metals used in manufacturing processes. As old factories closed and were demolished, techniques were developed for reclaiming their sites. It might not be possible to grow food in the contaminated soil, but the land could be made safe for building and some recreational use.

The Stockholm Conference was not held in a vacuum or purely in response to environmentalist pressure groups. Already people across the industrialized nations were demanding improvement in their physical, chemical, and biological surroundings, and their governments were responding. Prior to the conference, a few governments had created ministries or agencies with overall responsibility for environmental protection and improvement. In the years following Stockholm, many more governments followed. The U.S. Environmental Protection Agency may have been the first. It was established in July 1970 in response to the growing public demand for cleaner air, water, and land. The United Kingdom's Department of the Environment was formed on October 15, 1970, through the merger of the Ministry of Housing and Local Government and the Ministry of Public Building and Works. At first the new department was concerned more with the built than the natural environment, but its brief soon expanded to include pollution reduction and wildlife protection.

By the start of the 21st century, the world continued to face serious environmental problems, but great progress had been made nationally, regionally, and globally, and more was in prospect. Gross air pollution due to smoke is no longer a problem in most industrial cities, and although traffic fumes pollute the air, the degree of pollution is monitored and measures are available to reduce levels when necessary. Factories are no longer permitted to discharge their untreated effluents into rivers or lakes. Accidents happen, of course, but systematic pollution is being brought under control. International treaties help governments control pollution that crosses national frontiers or affects international air or water. Wildlife continues to face threats arising from loss of habitat and in some cases from hunting, but the dangers are well known. International agencies and governments are making strenuous efforts to improve wildlife protection. And, of course, the voluntary environmental and conservation movements continue to flourish. The future for the global environment is probably much better than the more pessimistic environmentalists suppose.

# Conclusion

*Ecology, the scientific study of natural communities, began to* emerge in the 19th century, when interest in natural history and conservation met and reacted with Darwinian evolutionary theory. Individual species of plants and animals inhabit particular places where conditions suit them. They are adapted to their environment, and adaptation is an evolutionary process. At one level, therefore, evolution by means of natural selection is an ecological theory (*see* "Evolution by Means of Natural Selection" on pages 90–96). The science developed further through the 20th century with the expansion of research into genetics.

An evolutionary theory that involved adaptation was one necessary precondition for the development of ecology, but it was not a sufficient condition. Scientists also needed a recognized, standardized system for classifying and naming species. Such a system developed over many years and culminated in the work of Linnaeus (*see* "Linnaeus and Biological Nomenclature" on pages 54–61). A tradition of caring about the countryside and its inhabitants supplied a third strand in the development of the new science.

As it developed, ecology has always remained close to these three sources of its original inspiration. Like most other scientists, a modern ecologist spends a good deal of time indoors, constructing and interpreting computer models of the systems being studied. The work requires a high level of statistical competence. That does not mean, however, that ecologists ever lose the fascination for the natural world that first attracted them, and most, probably all, are firmly committed to the conservation of wildlife and natural habitats.

This book has attempted to trace an outline of how ecology began and the way it has developed. In years to come, ecologists will deepen their understanding of how a natural community functions and the role that each of its members fills. Deeper understanding will add to the accumulating sum of human knowledge, of course, but it will do much more than that. It will allow ecologists to predict with some hope of accuracy how an ecosystem will respond to outside events. That will improve the skill and precision with which developments can be planned in such a way as to avoid harming the natural world.

# GLOSSARY

**alga (pl. algae)** a simple plantlike organism, lacking stems, leaves, or roots, which performs **photosynthesis**; most algae are single-celled, but seaweeds are also algae.

**annual plant** a plant that completes its life cycle from germination to the production of seed and the death of its roots, stems, and leaves in a single year.

**arthropod** a member of the phylum Arthropoda, comprising animals with jointed limbs, including all crustaceans, spiders, mites, insects, centipedes, millipedes, and horseshoe crabs, as well as some smaller classes and the extinct trilobites and eurypterids (water scorpions).

**assart** to convert an area of forest or common land to private arable land or pasture; farmland created in this way.

**autecology** the **ecology** of individual organisms and of populations usually comprising one or two species.

**biocoenosis** the community of living organisms in an **ecosystem.**

**biogeochemical cycle** the movement of a chemical element between the physical environment and living organisms.

**biogeography** the study of the geographic distribution of plants and animals.

**biome** the largest biological unit recognized, covering a large area and coinciding approximately with a climatic region; deserts, temperate forests, boreal forests, tropical grasslands, and temperate grasslands are examples of biomes.

**biosphere** that part of the Earth in which living organisms interact to form a steady-state system; an **ecosystem** extending over the whole planet.

**carbonate rock** rock containing carbon in the form of carbonate ($CO_3$) compounds.

**carrying capacity** the largest number of individuals an environment with limited resources can support.

**chase** in England, a formerly royal forest that has passed into private ownership.

**chlorophyll** the green pigment found in green plants, **algae,** and **cyanobacteria** that absorbs light, releasing an electron that triggers the process of **photosynthesis.**

**climax** the final stage in a plant **succession,** when the vegetation is in equilibrium with its chemical, physical, and biological environment and, in the absence of external perturbation, further changes in its composition occur slowly if at all. There are two concepts of a climax: **monoclimax** and **polyclimax.**

**clone** a group of genetically identical individuals derived from an ancestor asexually.

**community ecology** the study of the relationships within a biological community, classifying and arranging them in order, to determine how members of the community interact.

**competitive exclusion principle (Gause principle)** the principle that two or more species that utilize the same limited resource in the same way cannot coexist in the same stable environment, because one species will outcompete its rivals or eliminate them in some other way.

**consumer** an organism that feeds on living or dead organic material.

**coppicing** cutting trees close to or just below ground level to stimulate the growth of many poles.

**cotyledon** seed leaf; a leaflike structure that emerges from a germinated seed and is later replaced by true leaves.

**cuticle** *see* **exoskeleton.**

**cyanobacteria** bacteria that contain **chlorophyll** and carry out **photosynthesis.** Some live independently, others form colonies, and some join together to form long filaments.

**density current** a current produced by differences in density between adjacent bodies of water.

**diatom** a marine **alga** enclosed in an elaborately patterned **frustule.**

**dune slack** a flat-bottomed area among sand dunes where the water table is close to the surface.

**ecological genetics** the genetics of the way populations of organisms relate to their environment.

**ecology** the scientific study of the relationships among living organisms and between living organisms and their living and nonliving environment.

**ecosystem** a discrete unit comprising living and nonliving components that interact to form a stable system.

**endemic** found nowhere else.

**epiphyte** a plant that grows on the surface of another plant, using its host only for support so it is not a parasite.

**erratic** a boulder or gravel deposit that has been transported by glacial action to the place where it is found and that is therefore of a different type from the underlying bedrock.

**Eukarya** in biological classification, the domain that includes all **eukaryotic** organisms: Plantae (plants), Animalia (animals), Fungi, and **Protista.**

**eukaryotic** describes a cell possessing a distinct nucleus enclosed by a double membrane and other features such as mitochondria and ribosomes, or organisms composed of such cells.

**eusocial** highly social.

**exoskeleton (cuticle)** the horny outer covering that encloses the bodies of all **arthropods.**

**exploitation competition** competition between two or more species for a resource all of them need in which one of the species is more efficient than its competitors at accessing the resource and therefore comes to dominate it.

**floral province** a geographically large area supporting a distinctive type of vegetation with many **endemic** species.

**foredune** the side of a coastal sand dune that faces the sea or lake.

**frustule** the cell wall of a **diatom,** containing silica. It is made in two overlapping halves.

**Gause principle** *see* **competitive exclusion principle.**

**geomorphologist** a scientist who studies landforms and their origins.

**geophysiology** the scientific study of the Earth as a total system, comprising all of its living and nonliving components.

**guano** accumulated bird droppings found along the South American western coast and used as a fertilizer.

**herbarium** a collection of dried and pressed plants, identified taxonomically and with information about when and where they were gathered.

**inclusive fitness** the evolutionary fitness of an organism, taking account of the success of all of its kin as well as its own success.

**interference competition** competition between two or more species for a resource all of them need in which one of the species denies the others access to the resource.

**island biogeography** a theory stating that the number of species on an island is determined by immigration from the nearest mainland and extinction; when these reach equilibrium, the total remains constant although the composition of the community changes.

**liana** *see* **liane.**

**liane (liana)** a free-hanging, wiry, climbing plant.

**limnology** the scientific study of freshwater lakes and rivers.

**logistic equation** a mathematical equation for calculating the rate at which a population in an environment with limited resources grows toward the **carrying capacity.** The equation is: $dN/dT = rN((K–N)/K)$, where $N$ is the number of individuals, $T$ is time, $r$ is the rate at which the population is capable of increasing, and $K$ is the carrying capacity of the environment.

**metamorphosis** the radical transformation from the larval to adult form of an invertebrate animal.

**monoclimax** a **climax** resulting from a **succession** that leads to a definite type of plant community, its composition being determined by climate.

**mutualism** an intimate relationship between two species that benefits both.

**niche** the function an organism fulfils in its environment, including the frequency with which it is present in a particular habitat and the amount of time it spends there, and the resources it utilizes.

**null hypothesis** an assumption that the opposite of an expected experimental result is true. This reduces the likelihood of reaching a false conclusion because a result will be accepted only if it departs significantly from that predicted by the null hypothesis.

**ontogeny** the development of an individual animal from the fertilization of the egg to adulthood.

**optimum foraging theory** a theory stating that as an animal moves across its territory obtaining food it makes decisions that maximize the amount of food it finds or that improve its foraging efficiency in some other way.

**order bed** a bed in a botanical garden in which the plants are grouped taxonomically or because they have particular uses, for instance fiber plants, medicinal plants, etc.

**parthenogenesis** development of an egg without fertilization by a male.

**perennating bud** bud from which growth resumes on a plant that has died down during the winter.

**perennial plant** a plant that lives for more than two seasons and, when mature, usually produces seeds annually.

**phenology** the study of the dates of producing leaves, flowering, and setting fruit in plants; the study of the effect of climatic change on the seasonal occurrence of such events and also of animal migration.

**pheromone** a chemical substance that an animal produces and releases into the environment and that induces a response in another animal of the same species.

**phloem vessel** a tube made from cells linked end to end that transports sugars made by **photosynthesis** to all parts of the plant.

**photosynthesis** the process by which green plants and some bacteria use the energy of sunlight (*photo-*) to drive a series of chemical reactions that produce (*synthesize*) carbohydrates (represented as $CH_2O$) from water ($H_2O$) and carbon dioxide $CO_2$). The overall process can be summarized as:

$$6CO_2 + 6H_2O \xrightarrow[\text{light}]{\text{chlorophyll}} C_6H_{12}O_6 + H_2O + 6O_2\uparrow$$

The upward arrow indicates that oxygen is released into the air; $C_6H_{12}O_6$ is glucose.

**phylogeny** the evolutionary history of an organism.

**physicotheology** the belief that the study of nature can reveal God's plan in creating communities of plants and animals in which each species performs a particular function.

**phytology** the study of plants.

**phytoplankton** *see* **plankton.**

**phytosociology** the classification of plant communities according to the characteristics and relationships of and among the plants within them.

**plankton** the community of organisms inhabiting the upper waters of lakes and the sea that drifts with the movements of the water. **Algae** and **cyanobacteria** perform **photosynthesis** and comprise the phytoplankton; predators and organisms that feed on the phytoplankton comprise the zooplankton.

**pollarding** the technique of cutting off the top of a tree about 7 feet (2 m) above ground level to produce a crop of poles while allowing livestock to graze beneath.

**polyclimax** a **climax** in which the composition of the vegetation is determined by a number of factors and changes in response to changes in one or more of the factors controlling it.

**population genetics** the study of heritable variations among members of a population.

**primary consumer** a **consumer** that feeds on plants.

**producer** in **ecology,** an organism that synthesizes organic substances from inorganic substances; green plants and **cyanobacteria** are producers.

**production** in **ecology,** the total amount of organic material synthesized in an **ecosystem** over a given time. In energy studies, the amount of plant growth during a given time, excluding reproductive structures such as flowers, fruits, and seeds.

**Protista** in biological classification, a kingdom in the domain **Eukarya** that includes all single-celled **eukaryotic** organisms; these may resemble plants or animals.

**Protozoa** phylum of single-celled eukaryotic (**Eukarya**) organisms, some of which resemble plants, others resembling animals. Many Protozoa are free-living, but among those that are not, some are disease-causing parasites.

**quadrat** the basic ecological sampling area for studying plant communities, commonly $1m^2$ for grassland but larger for woodland. The plot is marked on the ground, and the researcher counts every plant of every species inside the boundary.

**radiolarian** a single-celled protozoon (*see* **Protozoa**) with silica cell walls.

**relevé** the basic field recording unit in **phytosociology**; it should be an area with uniform vegetation, topographical relief, and type of soil, and the record includes information about the soil and other environmental features.

**respiration** a sequence of chemical reactions in which an organism oxidizes organic compounds with the release of energy; it is the reverse of **photosynthesis.**

**rhizome** an underground plant stem.

**secondary consumer** an animal that feeds on **primary consumers.**

**secondary-growth forest** forest that has grown up naturally on land from which the original, primary forest was cleared.

**seiche** a stationary or standing wave in an enclosed body of water such as a bay or lake.

**social Darwinism** the theory, first proposed by Herbert Spencer (1820–1903), that human societies evolve through the survival of its fittest members and social evolution amounts to progress leading to improved living conditions for all.

**stoma** *see* **stomata.**

**stomata** pores through which plant leaves exchange gases; pores through which **arthropods** breathe.

**succession** the sequence of changes that takes place in a plant and animal community as the community adjusts to environmental changes or as new species arrive to alter its composition.

**sucker** an underground shoot growing from the root or base of the stem of a plant.

**superorganism** a group of individuals that together exhibit characteristics similar to those of a single organism.

**symbiosis** a situation in which two dissimilar organisms live together in close association; the relationship is usually assumed to be mutually beneficial.

**synecology** the study of whole plant and animal communities, including the alteration of **ecosystems** and **ecosystem management.**

**system** a group of objects that work together in such a way that a change in one component affects the group as a whole.

**systems ecology** the branch of **ecology** that studies **ecosystems** as complex **systems** regulated by feedbacks and with characteristics that cannot be deduced from the study of the individual components of the system.

**taxonomy** scientific classification, especially of biological organisms.

**tertiary consumer** an animal that feeds on **secondary consumers.**

**tree rings** alternately pale and dark rings, visible in a cross section through a tree trunk, that mark the annual spring (pale ring) and late summer and fall (dark ring) growth of the tree.

**trophic** pertaining to food or nutrition.

**wildlife management** the management of an area in such a way as to maintain certain of its animal populations at a desirable level determined by the managers.

**woodward** in medieval England, a forest keeper in charge of the growing timber.

**zooplankton** *see* **plankton.**

**zooxanthellae** any yellow-colored, single-celled **algae**; the term is no longer considered to have any taxonomic meaning.

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