Milestones in Ecology

Compiled by Christopher Morris

This timeline presents a view of the successive advancement of the field of ecology, first through earlier developments that provided a foundation for the field and then through developments within the formal discipline of ecology itself, from the late 1800s onward. The timeline concludes with a cutoff date in the late twentieth century, based on the principle that contemporary developments need a certain interval of time before their significance can be properly evaluated.

500,000 BC. Proposed date for the earliest use of fire in a controlled manner, the first major alteration of the natural environment by human activity. By about 3000 BC, many forest regions of the Middle East will be stripped of trees for the fuel demands of the Bronze Age.

8000 BC. Estimated time for the beginnings of agriculture, crop irrigation, and village formation in various areas of the world, especially in parts of the so-called Fertile Crescent such as Mesopotamia and the Nile Valley. Evidence also indicates that plants such as gourds were being cultivated at about the same time in the Oaxaca Valley of Mexico.

ca. 2000 BC. The Indus Valley civilization, one of the three great sites of early civilization along with Mesopotamia and Egypt, declines and eventually collapses. Cited as a leading cause of this is the large-scale removal of forests, which is thought to have shifted the habitat preferences of the mosquito *Anopholes stephansi,* a dangerous malaria vector, from forest to urban areas.

900s BC (?). The Bible states in Genesis 1:26: "And God said, Let us make man in our image, after our likeness: and let them have dominion over the fish of the sea, and over the fowl of the air, and over the cattle, and over all the earth, and over every creeping thing that creepeth upon the earth." This passage has been interpreted in contrasting ways in the modern era, on the one hand as the Christian basis for the concept of environmental stewardship, and conversely, as a God-given right to exploit the natural world for human benefit.

500s BC. Ancient Chinese writers describe feeding patterns in animal communities with aphorisms such as "The large fish eat the small fish"; "Large birds cannot eat small grain"; and "Each hill can shelter only a single tiger." In the twentieth century, animal ecologist Charles Elton will cite these sayings to show ancient awareness of the principle of food pyramids.

400s BC. The Greek philosopher Empedocles postulates that animals had originally been formed at random from individual parts, with those in which the parts formed a natural body shape surviving and reproducing over time, whereas those with mismatching parts died out. This concept of survival of certain body types and extinction of others roughly anticipates the nineteenth-century theory of natural selection.

400s BC. Herodotus, known as the father of history, reports on the wildlife he observes in areas of the Mediterranean. He identifies an example of mutualism, involving the Nile crocodile (*Crocodylus niloticus*) and a bird (the Egyptian plover, *Pluvianus aegyptius*) that removes and eats parasitic leeches in the crocodile's mouth. Herodotus also describes a balance-of-nature concept by noting that prey animals such as the rabbit have greater reproductive capacity than the predators that feed on them.

ca. 380 BC. A striking example of resource depletion is described by Plato, who decries loss of forest cover, and subsequent erosion, in the mountains of his native region of Attica. He portrays the area as "A mere relic of the original country. . . . What remains is like the skeleton of a body wasted by disease. All the rich soil has melted away, leaving a country of skin and bone."

300s BC. Aristotle establishes a classification system for animals, placing those with red blood in a different category from those without blood. This in effect corresponds to the contemporary distinction between vertebrates and invertebrates. He further divides the blooded animals into five groups similar to the modern system of mammals, birds, reptiles, amphibians, and fish.

300s BC. Chinese philosophers of the Taoist (Daoist) tradition develop a concept of living as one with nature, based on the idea that humanity is only a single component of the wholeness of the natural world, rather than the master of it. Restraint is urged in the use of resources to maintain the harmony and balance of nature. Taoism has thus been described as a model for the modern environmental philosophy of deep ecology.

ca. 300 BC. Aristotle's pupil Theophrastus produces an exhaustive study of plants, describing them according to such criteria as method of reproduction, size, habitat, method of cultivation, practical uses, and appearance, smell, and taste. This is considered the first significant step in the systematic classification of plant life.

ca. 220 BC. The Qin Dynasty of ancient China enacts the world's earliest known environmental protection laws. According to documents recently discovered, bans or restrictions were placed on the cutting of trees, the burning of grass or picking of germinating plants, the killing of baby animals and birds, and the use of poison, traps, or nets to catch fish and game.

100s BC. Ancient Rome provides contrasting examples of the management of ecosystem services. On one hand, the Romans successfully manage and conserve water through an elaborate system of aqueducts and water fountains. On the other hand, they fail to properly manage forest resources, and evidence suggests this deforestation is one of the causes of the eventual collapse of the Roman Empire.

ca. AD 65. Greek physician Dioscorides travels widely in the area of the Mediterranean and Asia Minor and writes *De Materia Medica,* a five-volume compendium on "the preparation, properties, and testing of drugs." In this work he describes more than 600 different plants that have pharmacological effects and establishes the practice of organizing botanical information on a species-by-species basis.

AD 800s. The Arab scholar Al-Jahiz provides the first explicit description of a food chain, stating that "All animals, in short, can not exist without food, neither can the hunting animal escape being hunted in his turn." He also is among the first to describe the effect of environmental factors on animal life.

1100s. Ibn al-'Awwam, an Arab agriculturist active in Moorish Spain, writes a comprehensive encyclopedia of botany in which he discusses hundreds of different kinds of crop plants, including 50 types of fruit trees. This work includes valuable information on soil science, fertilization, grafting, and plant pathology.

1100s. The Cistercians, a Roman Catholic monastic order, develop methods of sustainable agriculture that allow their monasteries to derive all necessary sustenance and income from their own farm production. In particular, they are noted for the practice of an early form of restoration ecology, converting desolate or abandoned terrain into fertile agricultural land.

early 1200s. St. Francis of Assisi becomes widely known for his love of nature. According to legend, he is able to gather flocks of birds around him and preach to them. He comes to represent the concept of living in harmony with the environment rather than trying to dominate it.

1240s. Frederick II, emperor of the Holy Roman Empire, publishes a six-volume treatise entitled *De Arte Venandi cum Avibus* [*The Art of Hunting with Birds*]. It is lavishly illustrated and contains many valuable observations on avian biology, dealing with topics such as comparative anatomy, feeding habits, characteristic habitats, and diurnal/nocturnal patterns.

1273. King Edward I of England enacts what is considered the first air pollution control law. The law bans the use of coal for fuel within the city of London. It applies to "sea coal," a low-grade form of soft coal that exudes excessive smoke.

ca. 1300. Forests of England and France have become depleted to such an extent that wood has to be imported from other countries. Demand for wood comes not only for heating and building but also for industrial uses such as ironworking, brewing, dyeing, and glassmaking.

before 1492. Native Americans engage in the cultivation strategy of the "three sisters" (corn, beans, and squash) over large areas of the Americas. They also practice land-use management through the controlled burning of forests and grasslands, which promotes the success of fire-resistant (or fire-dependent) plant species.

1493. Christopher Columbus returns to Spain from his momentous voyage to the West Indies, carrying specimens of various plants, birds, and animals previously unknown to the Old World. These include important food plants such as maize (corn), sweet potatoes, peppers, bananas, and pineapples. Columbus is also said to be one of the first to note that forests influence and enhance rainfall, through his observations of the landscape of the Azores and Canaries.

1503. The German artist Albrecht Dürer creates a watercolor known as "The Large Piece of Turf," which is described as the first work of art with an ecological theme. Before this, artists had included plants as background for scenes with human subjects, but Dürer's painting realistically portrays a plant community separate from human society.

1543. Andreas Vesalius, a Flemish physician, publishes *De Fabrica Corporis Humani* [*Concerning the Structure of the Human Body*], a book that founds the scientific discipline of anatomy. The influence of Vesalius extends beyond anatomy as his work inspires various similar studies in zoology, as by Pierre Belon on birds (1555) and Conrad Gesner (see next).

1556. Swiss naturalist Conrad Gesner completes the fourth volume of his *Historiae Animalium,* a far-ranging study of animal life. The books are profusely illustrated and deal with, respectively, mammals, reptiles and amphibians, birds, and fish and other aquatic animals. Gessner's work is regarded as the beginning of the field of vertebrate zoology.

1583. Italian scientist Andrea Cesalpino publishes *De Plantis Libri XVI,* which is considered the first textbook of botany in that he studies plants for their own sake rather than in terms of their applications in medicine, agriculture, and horticulture. In this book, he employs a system of binomial nomenclature that anticipates the work of Linnaeus by almost two centuries.

1603. The Lincean Academy is founded by Federico Cesi in Rome. Galileo Galilei will become a member in 1611. This is one of the first scientific communities, and it carries out important research in fields such as entomology and paleobotany, especially with the use of the newly invented microscope.

1623. In his book *Pinax Theatri Botanici* [*An Illustrated Exposition of Plants*], Swiss botanist Gaspard Bauhin refines the earlier work of Cesalpino in taxonomy, by classifying thousands of plants according to their genus and species names.

1661. English diarist John Evelyn publishes one of the first known books on air pollution, entitled *Fumifugium, or the Inconveniencie of the Aer and Smoake of London Dissipated.* To improve the poor air quality of London, he suggests alternative energy (burning aromatic woods instead of sea coal) and an early version of the greenbelt concept (moving energy-intensive industries away from the city center and replacing them with gardens and orchards).

1662. John Graunt founds the scientific field of demography. He makes a rigorous study of the population of London, compiling statistics for birth and death rates, age distribution, and sex ratio. He then extends this methodology to the animal kingdom by using similar criteria to study fish populations.

1665. Robert Hooke publishes *Micrographia*, a book that describes the microbiological environment for the first time. Hooke studies sections of the cork plant and identifies patterns of tiny cylindrical structures therein, which he likens to small enclosed rooms and thus calls *cells*.

1668. Francesco Redi of Italy makes the first step in disproving the theory of spontaneous generation by conducting an experiment to show that maggots cannot appear spontaneously on rotting meat. He is influenced by the thinking of the physiologist William Harvey, who had stated *"Ex ovo omnia"* ("Everything comes from the egg").

1669. Dutch microscopist Jan Swammerdam conducts extensive research on insects and produces accurate descriptions of the anatomy and life history of numerous species, accompanied by meticulously detailed drawings. He determines that the successive forms of egg, larva, pupa, and adult are not different organisms but actually different life stages of one organism.

1669. The Danish scientist Nicholas Steno recognizes that "tongue stones," unknown solid objects found in rock, look very much like the teeth of living sharks. He concludes that these tongue stones are not mineral matter but the remains of animal and plant organisms, thus establishing the organic origin of fossils.

1674–1683. Using a microscope of his own construction, Anton van Leeuwenhoek is the first person to detect and describe "animalcules," known today as bacteria or protozoa, which he views in such media as rainwater, lake and well water, and the human mouth. His discoveries awaken humankind to a previously unknown world of microorganisms and establish the science of microbiology.

ca. 1681. The flightless dodo bird of the Raphidae family becomes extinct on its native island of Mauritius in the Indian Ocean. This is attributed to a combination of hunting by European settlers, deforestation of habitat by these settlers, and predation by exotic species introduced by the settlers, such as pigs and monkeys. This is the first notable extinction of a species in historic times, and it heightens awareness of the effect of human activity on the natural world.

1686. English naturalist John Ray publishes the first of three volumes describing nearly 20,000 plant species. He classifies plants according to overall morphology and focuses on the species as the fundamental level at which organisms should be distinguished from one another. He also notes that the fossil record seems inconsistent with the Biblical account of the Great Flood.

1700s. European explorers and naturalists in the Americas encounter many species of animals and plants not found in the Old World, though some are mistakenly linked to similar known species (e.g., the American bison, the wild turkey). In particular, they note the greater general abundance of wildlife in the New World than in Europe.

1730s. French entomologist René A. F. de Réaumur studies the reproductive rate of aphids and calculates that each individual is capable of producing about 6 billion offspring over successive generations, within a period of just 6 weeks. Because such a population does not exist, he speculates that there must be natural limiting factors to regulate population.

1735. Carolus Linnaeus publishes the first edition of *Systema naturae* [*Systems of Nature*]. In this work, he is the first to consistently use a system of binomial nomenclature based on observable physical characteristics, and thus he is regarded as the father of the modern field of taxonomy.

1741. German naturalist and explorer Georg Wilhelm Steller describes an aquatic herbivorous mammal that becomes known as Steller's sea cow (*Hydrodamalis gigas*), which he observes near the Asian coast of the Bering Sea. By 1768 Steller's sea cow will be hunted to extinction, in a classic example of the rapid disappearance of a species through overexploitation.

1749. George-Louis Leclerc, Comte de Buffon, publishes the first of 44 volumes of his *Histoire naturelle* [*Natural History*]. He defines the concept of a species on the basis of reproductive exclusivity, and he would later be cited by Darwin as a major influence on his concept of evolution. Buffon also considers issues such as the role of geography in biodiversity, the relationship of humans to other primates, and the formation of the earth from molten matter.

1751. Pierre-Louis Moreau de Maupertuis publishes *Système de la Nature,* in which he records his views on heredity, in particular the occurrence of mutant traits. He also will be recognized as a forerunner to Darwin for his observation that stronger animals in a population produce more offspring.

1760. The prominent Swiss mathematician Leonhard Euler develops an equation to describe and forecast the dynamics of age-structured populations. This model for population growth rate will be refined by Alfred Lotka in the twentieth century (and thus become known as the Euler-Lotka equation).

1764. Linnaeus reexamines his earlier belief that species are fixed and immutable; he especially notes obvious examples of hybridized plants. He theorizes that God must have created only a limited number of species, which hybridized over time to form the great diversity of species existing in the present day.

1773. Georg Foster, a botanist accompanying Captain James Cook to New Zealand, provides one of the earliest descriptions of a species invasion unintentionally caused by human activity. He notes that canary grass, a plant native to the Mediterranean, has become established in several sites, possibly through windborne seeds from Cook's vessel in an earlier voyage.

1774. Joseph Priestley publishes his description of oxygen, which he and several others had independently discovered 2 years earlier. In his experiments, Priestley establishes that plants convert the carbon dioxide breathed out by animals back into oxygen, thus providing the basis for an understanding of photosynthesis. He also learns that mice will die in a sealed environment if plants are not present to

reoxygenate the air, indicating that the collective metabolic activities of species in an ecosystem will influence its biogeochemistry.

1775. Linnaeus states a balance-of-nature concept, declaring that "In order to perpetuate the established course of nature in a continued series, the divine wisdom has thought fit, that all living creatures should constantly be employed in producing individuals; that all natural things should contribute and lend a helping hand to preserve every species; and lastly, that the death and destruction of one thing should always be subservient to the restitution of another."

1779. Dutch physiologist Jan Ingenhousz refines the findings of Priestley concerning the ability of plants to reoxygenate the air by establishing that this occurs only in the presence of light. He also learns that photosynthesis takes place through the actions of the green plant pigment chlorophyll, rather than the entire plant.

1785. Scottish geologist James Hutton rejects the prevailing idea of the time that the Earth has an age of about 6000 years. He states that the time required for the gradual formation of the natural structures of the planet has to be much longer than this, so long in fact that the age of the Earth is inconceivably great.

1789. Clergyman Gilbert White publishes *The Natural History and Antiquities of Selborne,* a comprehensive and precise description of the natural environment in and around his hometown in southern England. It becomes the most widely read book of natural history ever published in the English language, and it has remained in print continuously up to the present day.

1794. Erasmus Darwin develops one of the first formal statements of the theory of evolution. In the form of a poem, he presents the idea that microorganisms in the ocean evolved over successive generations into the plant and animal life of the present day. However, he does not conceive of natural selection as the mechanism driving this process, something that will be left to his grandson Charles.

1798. French scientist Georges Cuvier publishes a set of drawings showing that there is a significant difference between the jaw structure of an Indian elephant and that of a mammoth, indicating that the mammoth is an extinct animal and not a different type of elephant. This definitely establishes the fact of extinction; before Cuvier the general view was that species that had apparently vanished must still be living somewhere else on Earth.

1799. Baron Alexander von Humboldt, a Prussian naturalist, begins his 5-year exploration of the colonial empire of Spain in the New World. He carries out many activities of zoological, botanical, and ethnographic research, including the collection and documentation of more than 60,000 tropical plants. Humboldt strives to describe his findings within the context of a single integrative science that unites all forms of natural phenomena. This provides the foundation for the current holistic approach to describing the complexity of the Earth's environmental system.

1800s. The nineteenth century experiences a significant rise in the level of carbon dioxide gas in the atmosphere, according to later measurements of ancient ice. This will be attributed to the significant increase in fossil fuel use associated with industrialization, population growth, and improved living standards.

1801. In *Systeme des animaux sans vertebres* [*System for Animals Without Vertebras*], Jean-Baptiste Lamarck becomes the first to provide a rigorous classification system for *invertebrates* (a term he coins), comparable to that of Linnaeus for vertebrates.

1809. Lamarck presents what has been described as the first truly modern and comprehensive theory of evolution. He states that more complex life forms such as mammals evolved from simpler forms and that the behavior of organisms will cause unused body parts to degenerate or new parts to develop as needed for survival. His thinking differs from later evolutionary biologists in that he believes morphological changes in an animal during its lifetime can be passed on to its descendants.

1815. Appreciation for the natural world is expressed by the Romantic Movement, especially in the poetry of William Wordsworth and the journals of his sister Dorothy. The urbanization and extensive land clearance associated with the Industrial Revolution have made Europeans more conscious of the loss of natural habitat and brought greater intellectual awareness of Nature as an entity distinct from human civilization.

1817. Cuvier publishes the first edition of a monumental work on the animal kingdom, noted especially for his classification of animals into four large groups (vertebrates, mollusks, articulates, and radiates), each with a discrete type of anatomical organization. This departs from the earlier idea that animal life is arranged in a hierarchy of complexity from the simplest organisms up to humans.

1824. Through his studies of steam engines, French engineer Nicolas Léonard (Sadi) Carnot establishes that heat moves from a system of higher temperature to one of lower temperature and that through this process work is done. This provides the basis for the second law of thermodynamics (which will be formally stated by Clausius in 1850) and eventually leads to an understanding of energy flows in ecosystems.

1826. Thomas Robert Malthus publishes the final edition of *An Essay on the Principle of Population,* in which he contends that "The power of population is indefinitely greater than the power in the earth to produce subsistence for man." He argues that food supply cannot keep pace with population growth, and this "Malthusian" view inspires many subsequent analyses of the relationship between population and resources, in particular Darwin's ideas about natural selection.

1827–1828. John James Audubon's *The Birds of America* is published and becomes an immediate best seller. It includes superbly illustrated descriptions of nearly 500 bird species of North America and is generally regarded as the greatest illustrated book ever published. In the early twentieth century, a pioneering conservation group will honor the painter by taking the name The National Audubon Society.

1830. The first volume of *The Principles of Geology,* a landmark work by Scottish scientist Charles Lyell, is published in London. In it he promotes the principle of uniformitarianism, the idea that the visible features of the Earth were formed over vast time spans by physical processes that are the same as those taking place at the present time.

1831–1836. Charles Darwin, on his *Beagle* voyage, observes and describes the effects of biological invasion, in particular the presence in the Galápagos Islands of numerous European animal and plant species. Many of these observations lead to insights that will be incorporated into *On the Origin of Species*.

1836. Louis Agassiz studies the glaciers of his native Switzerland and observes that the effects of glaciation can be seen in other places where glaciers no longer are present. He then advances the idea that a great Ice Age occurred at some time in the past, during which huge glaciers covered much of the Earth's surface. Agassiz thus can be considered one of the first to recognize the phenomenon of climate change.

1838. Belgian mathematician Pierre F. Verhulst publishes what is known as the logistic equation to describe the maximum number of individuals an environment can support. He indicates that the factors that tend to limit population growth will increase in proportion to the ratio of the excess population to the overall population. In the 1920s this equation will be utilized by Raymond Pearl and Lowell Reed for their studies of historic population growth in the United States.

1838. German botanist August Grisebach examines plant communities in terms of their geographic distribution and their relationship to climate, an early example of the study of ecosystem structure and function. He also describes the forces that can affect plant distribution.

1840. Justus von Liebig publicizes the Law of the Minimum, which states that if all the essential nutrients but one are available in the quantities required for the growth of a plant, the deficiency of that one nutrient will prevent growth. Later scholars will apply this concept of the limiting factor to larger contexts such as ecosystems.

1842. Sir Richard Owen coins the term *Dinosauria,* meaning "terrible lizard," to describe a category of large extinct terrestrial vertebrates. Through history dinosaur bones had been discovered, but they were thought to be from mythical creatures or from giant forms of existing reptiles. It was not until the discoveries of Gideon Mantell and others in the early nineteenth century that dinosaurs were recognized as a distinct taxonomic group.

1847. Hermann von Helmholtz publishes *Uber die Erhaltung der Kraft* [*On the Conservation of Energy*], establishing that the amount of energy in the universe is constant and that energy can neither be created nor destroyed, only converted from one form to another. This becomes known as the first law of thermodynamics, and, like the second law (which actually was identified earlier), it will become fundamental to ecologists' understanding of bioenergetics.

1854. Henry David Thoreau publishes *Walden Pond, or Life in the Woods*, his account of a self-sustaining lifestyle apart from industrial society. Thoreau, with his mentor Emerson, will initiate an intellectual movement in North America comparable to that of Rousseau and the Romantic poets in Europe. This is based on the realization that the pastoral landscape, so long taken for granted, is threatened by human activity.

1858. Alfred Russel Wallace completes the manuscript of an essay presenting his conclusions concerning the origin and diversity of species. He sends the manuscript for review to a more prominent scientist, Charles Darwin, who notes the similarity with his own ideas on evolution, as yet unpublished.

1859. Darwin publishes *On the Origin of Species,* a book describing his theory of evolution by natural selection. It is greeted with great interest and controversy, and it becomes the foundation of a new form of biology. Its influence will eventually surpass that of any other book in the history of science, with the possible exception of Newton's *Philosophiae Naturalis Principia Mathematica.*

1859. Thomas Austin introduces two dozen European rabbits onto his property in the state of Victoria, Australia, for the purpose of sport hunting. In a classic example of unchecked population growth in an invasive species, within a decade the descendants of these rabbits will reach a population that numbers in the millions and spreads over much of the continent.

1862. English naturalist Henry Walter Bates recognizes and illustrates what will become known as Batesian Mimicry. This is the ability of a prey species to evolve a defense against a common predator through similarity of coloration and patterning with other species that are poisonous or otherwise less palatable.

1862. The theory of spontaneous generation, widely believed since the time of Aristotle and first challenged by Redi in the seventeenth century, is finally put to rest by Louis Pasteur. He shows that a sterilized broth will remain sterile as long as bacteria are prevented from entering it in some way, even if it is exposed to air.

1865. German physicist Rudolf Clausius introduces the concept of entropy (disorder or randomness) to measure the amount of energy available to do work. He establishes that entropy cannot decrease in a physical process and can only remain constant in a reversible process. This becomes formalized as the second law of thermodynamics, and it will come to have great influence on the thinking of ecologists.

1865. Gregor Mendel reads a paper summarizing his experiments with pea plants, dating back to 1854. During his lifetime his work is noted but not frequently cited, and its implications for the theory of evolution are not recognized. However, in the early twentieth century, his findings will be reexamined, and he will ultimately be described as the founder of the science of genetics.

1871. Darwin publishes *The Descent of Man,* in which he directly applies his principles of evolution to the human race. He states that "man is descended from a hairy, tailed quadruped, probably arboreal in its habits, and an inhabitant of the Old World." He describes this animal as a *Quadrumana*, an older term for the great apes.

1872. British scientist Robert Angus Smith publishes *Air and Rain: The Beginnings of a Chemical Climatology,* in which he summarizes his extensive investigations of precipitation throughout the British Isles. He reports high levels of acidity in the rainwater of large manufacturing cities such as Manchester and Glasgow. Smith employs the phrase "acid rain" to describe this.

1872. President Ulysses S. Grant signs into law an act establishing Yellowstone National Park, the first national park of the world. Located in the northwestern United States, it has a remarkable combination of unique geological features, striking landscapes, and abundant wildlife.

1873. London experiences the first in a series of "killer fogs" that are responsible for thousands of deaths. These occur sporadically until the mid-twentieth century, when stricter controls on emissions are finally enacted.

1873. The term *ecology* enters the English language, having been coined shortly before this in German as *Ökologie* by the biologist Ernst Haeckel. He combines two Greek terms meaning "household" or "dwelling" and "science" or "study." The concept is that ecology is "the study of the house of nature." The spelling *ecology* (as opposed to *oecology*) will be officially adopted as the correct English version in 1893.

1874. *Man and Nature, or Physical Geography as Modified by Human Action* is published by the American scholar George Perkins Marsh. As the title indicates, Marsh examines the role of human activity as an agent of environmental change, noting especially the desertification of once-fertile areas of the Mediterranean. He thus departs from the conventional view of the time that the physical landscape of the Earth is essentially the product of natural phenomena.

1875. Geologist Eduard Suess introduces the term *biosphere,* which he describes as "the place on earth's surface where life dwells." An alternate term, *ecosphere,* will be introduced in 1953. Today both words are also used to describe an enclosed, self-contained ecosystem.

1876. Alfred Russel Wallace produces a definitive work of biogeography, *The Geographical Distribution of Animals,* which provides support for the theory of evolution. In the companion work *Island Life* (1880), he blazes the trail for the study of island biogeography.

1877. Zoologist Karl Möbius studies natural oyster banks in the North Sea, employing what is thought to be the first use of the term *community* in the modern sense. He describes the complexity and interrelationships of an oyster bed community and recognizes that the nature of the community would be transformed if the population of any given species were to decrease or increase through human intervention.

1880s. The folk belief that "Rain follows the plow" encourages agricultural development in the Great Plains region of the United States. It was thought that plowing under native vegetation to plant crops such as wheat and corn will lead to increased rainfall, an idea that will be proved catastrophically wrong during the Dust Bowl era of the 1930s.

1881. German naturalist Karl Semper publishes *Animal Life as Affected by the Natural Conditions of Existence.* He provides an accurate description of a generalized food chain, outlining the pyramid of mass from plant material to herbivores to carnivores. This is regarded as one of the earliest studies of energy flows in nature.

1883. The German biologist August Friedrich Leopold Weismann emphasizes that inherited characteristics are transmitted only via the sex cells and not the somatic cells, thus discounting the Lamarckian idea of inheritance of acquired characteristics. He describes a special hereditary substance possessed by all organisms, which he calls germ plasm; this roughly corresponds to the modern understanding of DNA.

1883. Thomas Henry Huxley, known as "Darwin's Bulldog" for his fierce advocacy of the theory of evolution, declares that the abundance of fish is so great that the fishing industry cannot seriously impact general fish populations. He says that "The cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea-fisheries, are inexhaustible; that is to say that nothing we do seriously affects the number of fish. And any attempt to regulate these fisheries seems consequently . . . to be useless."

1887. American zoologist Stephen A. Forbes publishes "The Lake as a Microcosm," in which he writes, "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 forms a little world within itself." His description of the interrelationship of the organisms at a definable site leads to the development of the ecosystem concept as well as to modern ideas of food web interactions and of the analogy between wildlife and human communities.

1889. The importing of domestic cattle into Somalia provides an example of contrasting effects of an introduced species. On one hand, this leads to an epidemic of the viral disease rinderpest, causing the death of millions of domestic and wild ungulates. On the other hand, it has a positive impact in that the decimation of cattle in many regions removes a major host for Tsetse flies (*Glossina* spp.), the vector of destructive diseases including African sleeping sickness.

1889. William Temple Hornady publishes *The Extermination of the American Bison*, predicting the imminent demise of a species (*Bison bison*) that just half a century earlier was estimated to consist of at least 60 million individuals. This creates public support for saving the species, and in the twentieth century its numbers will rebound to several hundred thousand.

1892. America's first environmental advocacy group, the Sierra Club, is founded in San Francisco with 182 charter members. Famed naturalist John Muir is the club's first president. He pledges "to do something to make the mountains glad."

1893. The earliest book in English with the explicit term *ecology* in its title is published: Louis H. Pammel's *Flower Ecology*. Pammel will go on to publish a textbook simply called *Ecology* in 1903, and he will also become the mentor of the famous African-American botanist George Washington Carver.

1895. Johannes Eugenius Warming of Denmark publishes *Plantesamfund: Grundtræk af den økologiske Plantegeografi,* the first in-depth textbook on plant ecology. Based on a series of lectures at the University of Copenhagen, it describes plant communities throughout the world in the context of the environmental factors affecting them.

1896. Polish botanist Jozef Paczoski establishes the field of phytosociology, the study of the organization and distribution of plant communities. He later publishes a textbook dealing with the modification of the environment by plants through the creation of microenvironments.

1898. Andreas Schimper of Germany is credited with originating the term *tropical rain forest.* Building on the pioneering work of von Humboldt, he and others recognize that similar vegetation types arise under similar climatic conditions in different parts of the world, and they define basic principles of plant form and function to explain these global patterns.

1899. Henry Chandler Cowles of the University of Chicago studies in detail the plant life of the Indiana Dunes bordering Lake Michigan. He notes the natural changes that occur in this vegetation as the sand dunes recede or advance, and from this, he develops a formal concept of ecological succession.

1901. Swiss scientist François-Alphonse Forel publishes *Handbuch der Seenkunde,* based on his decades-long studies of the waters of Lake Geneva. This is the first textbook in the field of limnology and establishes it as a scientific discipline.

1904. Christen Raunkiaer, a student of Eugenius Warming, prepares a life-forms classification system for plants using quantitative methods. In this system plants are categorized according to the physical position and degree of protection of their perennating organs (buds) during adverse growing conditions. He observes that most plant species in a given community fall within the polar frequency categories of very common or very rare (Raunkiaer's Law).

1905. Conservation of the natural environment becomes government policy in the administration of Theodore Roosevelt. He establishes the U.S. Forest Service, headed by Gifford Pinchot, and creates many national parks and wildlife and bird refuges. Roosevelt recognizes that it is necessary to protect entire ecosystems in order to preserve certain endangered species.

1905. Frederic Edward Clements publishes *Research Methods in Ecology,* considered the earliest work to set out a systematic approach to ecological research. It emphasizes experimental evidence and advocates the use of mathematical and graphical presentations. At about this time he begins to use the term *ecotone,* or "zone of tension," to describe boundary areas between adjacent communities.

1905. The concept of a limiting factor in photosynthesis is shown by the British botanist Frederick Frost Blackman. The limitations on this process are the supply of carbon dioxide, the relative temperature, and the amount of light, and Blackman demonstrates that the rate of photosynthesis is controlled by whichever of these factors is least available.

1907. The term *eutrophication* is coined by the German scientist C. A. Weber to refer to the rich wetlands in Europe that receive nutrient runoff from surrounding areas. The term is then applied to lakes by Swedish limnologist Einar Naumann, roughly a decade later.

1908. What becomes known as the Hardy-Weinberg Principle is proposed independently by Godfrey Hardy of Britain and Wilhelm Weinberg of Germany. One of the basic concepts of population genetics, it states that the frequency of genotypes in a large random-mating population is simply the product of their relative frequencies. This indicates that gene pool frequencies are inherently stable unless evolutionary mechanisms cause them to change.

1912. Geneticist Sewall Wright publishes his first scholarly paper, on the anatomy of the trematode; his last paper will appear 76 years later. In the 1920s, Wright will introduce the concept of genetic drift, and he, along with J.B.S. Haldane and Ronald A. Fisher, will found the field of population genetics.

1913. Charles C. Adams publishes *Guide to the Study of Animal Ecology,* the first major work devoted specifically to this topic. He draws on research carried out in the Lake Superior area of northern Michigan (1905) and at Isle Royale (1909). Adams argues that the term *ecology* should become standard usage for animal studies as well as plants, saying "To use a different name for the same subject or process in botany and zoology is as undesirable as to use a different term for heredity in plants and animals."

1913. The *Journal of Ecology* is founded by the British Ecological Society as the first international, peer-reviewed ecological journal in the world. It will be joined in 1920 by *Ecology,* the flagship journal of the Ecological Society of America, which is the successor to an earlier publication *The Plant World* (founded 1897).

1913. Victor Ernest Shelford develops the Law of Tolerance, an extension of Liebig's Law of the Minimum. It states that for an organism to succeed in a given environment, conditions must remain within a maximum and minimum range of tolerance for that organism. In 1915 Shelford will help to organize the Ecological Society of America and will serve as its first president.

1914. The last known passenger pigeon (*Ectopistes migratorius*) dies in captivity in a Cincinnati zoo. This marks the end of a species that in the mid-nineteenth century was so numerous that a flock passing overhead could darken the sky for an entire day, in the manner of a solar eclipse. According to tradition, the last credible sighting of a passenger pigeon in the wild was by Theodore Roosevelt in 1907.

1916. Clements presents his view of ecological succession in *Plant Succession: An Analysis of the Development of Vegetation.* He conceives of a community as in effect a superorganism, whose component species are tightly bound together both in the present and in their common evolutionary history. This advances the idea of a community functioning as an integrated unit, with interactions among its plants, animals, microorganisms, and so on.

1917. Ornithologist Joseph Grinnell of the University of California establishes the concept of the ecological niche in his paper "The Niche Relationships of the California Thrasher." The word *niche* is from the Middle French *nicher,* meaning "to nest," and the term is used to indicate

that the ecological niche of a species is in effect its "nook" or "cubbyhole," i.e., its specific, limited, and accustomed place within a larger community.

1921. Olof Arrhenius, son of the famous physical chemist Svante Arrhenius, describes the species–area relationship. He counts the number of species occurring in different-sized units of vegetation for certain Swedish island systems and then presents the results as a mathematical formula. He observes that "the number of species increases continuously as the area increases."

1924. J.B.S. Haldane publishes the first of a series of papers under the title *A Mathematical Theory of Natural and Artificial Selection,* in which he offers a mathematical description of fitness. He defines individual fitness simply by reproductive success, i.e., the total number of offspring that the individual produces in a lifetime.

1925–1926. The mathematicians Alfred Lotka of the United States and Vito Volterra of Italy independently develop standard models to describe the interactions of predator and prey species. The so-called Lotka-Volterra equations demonstrate the inherent tendency of predator–prey populations to oscillate; e.g., a large predator population will reduce available prey to the point where predators decline from lack of food, but this will result in a population increase for the prey species and a subsequent resurgence of the predator.

1926. August Thienemann, a German limnologist, publishes a unique food web of lakes, in which he develops the basic concepts of nutrient cycling in water and food cycle relationships among producers, consumers, and decomposers. Thienemann had earlier observed that biodiversity is greater with habitat diversity and is reduced with habitat disturbance.

1926. Botanist Henry Gleason presents an alternative to the prevailing view of Clements that ecological communities are the result of tight species associations. He argues that a community is not an organic entity but rather "is merely the resultant of two factors, the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment . . . not an organism, scarcely even a vegetational unit, but merely a coincidence."

1926. Russian scientist Vladimir Vernadsky develops the modern concept of the term *biosphere* and notes the tendency of human activity to influence this entity. He states that all organisms on earth "are inseparably and continuously connected—first and foremost by feeding and breathing—with their material-energetic environment." Vernadsky also recognizes that the oxygen, nitrogen, and carbon dioxide in the Earth's atmosphere result from life processes.

1926. The Ecological Society of America creates a committee "charged with the listing of all preserved and preservable areas in North America in which natural conditions persist." The committee's report is published as *Naturalist's Guide to the Americas* (edited by Shelford). This is an early example of a "gap analysis" of protected ecosystems in southern Canada and the United States.

1926. Warder Clyde Allee begins a series of papers with the heading "Animal Aggregations." He concludes that there is a natural tendency for organisms of the same species to assemble in social groups and that negative effects can arise not only from overcrowding in a habitat but also undercrowding. He also proposes that animals will unconsciously cooperate in the interest of group survival, which he terms *proto-cooperation.*

1927. Charles Sutherland Elton publishes *Animal Ecology,* in which he stresses the importance of feeding (energy) relationships among organisms as the basis for understanding nature. Elton describes the niche of a species as "its place in the biotic environment, its relations to food and enemies," and he is credited with saying, "When an ecologist says 'There goes a badger,' he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said, 'There goes the vicar.'"

1930. British scientist Roy Clapham is reportedly the first to use the term *ecosystem* to describe the fundamental unit of nature. German entomologist Karl Friedrich had introduced the word *holocoen* for this concept in 1927, and a comparable term *biogeocoenosis* will be employed by the Soviet forest scientist Vladimir N. Sukachev in 1944. However, neither of these terms is as widely used as *ecosystem,* which becomes the standard word.

1930. The *Genetical Theory of Natural Selection* is published by Ronald Fisher, the first definitive effort to explain Darwin's evolutionary theories in a genetic context. This becomes a classic text of modern evolutionary biology and has been described as the single most important work in the field after *On the Origin of Species* itself.

1931. American economist Harold Hotelling develops a model for the efficient use of nonrenewable resources over time. According to Hotelling, it can be economically rational to degrade an ecosystem or deplete a species even when market prices reflect the true value of these resources. His approach to resource theory has become the dominant one in contemporary ecological economics.

1932. Josias Braun-Blanquet of Switzerland develops a standard method of sampling for vegetation classification, based on the visual abundance of a species within a defined area. He uses this *relevé* method to classify much of the vegetation of Europe.

1934. Russian biologist Georgyi Frantsevitch Gause presents pioneering research on competition for resources. His experiments on microbial communities show that two similar species will grow adequately when cultured separately, but in mixture, one will drive the other to extinction. This indicates that when two populations with ecologically similar requirements compete for limited resources in a stable environment, eventually one will persist and the other disappear.

1935. A. J. Nicholson and V. A. Bailey of Australia publish "The Balance of Animal Populations," presenting a model that can be used to describe the population dynamics of a coupled host–parasite (or predator–prey) system. A central characteristic of the Nicholson-Bailey model is that both populations undergo oscillations with increasing amplitude until first the host dies out and then the parasitoid population as well.

1935. British scientist Arthur G. Tansley refines the term *ecosystem,* which had been coined 5 years earlier at his request by his colleague Roy Clapham. Tansley promotes the use of *ecosystem* as the most useful term for an interactive system consisting of all the organisms functioning in a given area and all the physical (nonliving) factors affecting the area.

1935–1937. Clements publishes two papers in which he describes how human activity has disrupted the climax community of the Great Plains, leading to the Dust Bowl conditions that exacerbated the Great Depression in the United States. He and others recommend an organismic approach to land use in which the natural grasslands will be saved or restored.

1937. Theodosius Dobzhansky, a Ukranian-American geneticist, publishes *Genetics and the Origin of the Species*; this effectively provides the link between the Darwinian theory of evolution through natural selection and the Mendelian theory of mutation in genetics. Dobzhansky will later become known to the general public through his 1973 paper "Nothing in Biology Makes Sense Except in the Light of Evolution," which is often cited as a dismissal of the antievolution worldview known as creationism.

1938. British engineer Guy S. Callendar studies historic records of temperature and determines that a warming trend is taking place. He compares this with historic measures of CO_2 concentrations and concludes that an increase in CO_2 levels correlates with this warming. Callendar then publishes "The Artificial Production of Carbon Dioxide and Its Influence on Climate," in which he directly implicates fossil fuel combustion as an agent of climate change.

1939. Frederic Clements and Victor Shelford collaborate on *Bio-Ecology,* which is intended to correlate plant ecology and animal ecology with the interest of advancing the science of ecology in general. They argue for the importance of plant–animal interactions within what Clements refers to as the *biome,* which is defined as "an organic unit comprising all the species of plants and animals at home in a particular habitat."

1939. Paul Hermann Müller of Switzerland develops the powerful organic insecticide DDT, which proves very effective in controlling insect populations that are the vectors for diseases such as malaria and typhus. In 1948 Müller will receive the Nobel Prize for this achievement, but the use of DDT will later become controversial because of its perceived detrimental effects on wildlife.

1940. Chancey Juday, an American aquatic scientist, publishes a study of the energy budget of lakes, based mainly on extensive studies carried out by himself, Edward A. Birge, and others at Lake Mendota, Wisconsin. Birge and Juday develop the concept of primary production, i.e., the rate at which food energy is generated, or fixed, by photosynthesis.

1942. Ernst Mayr presents the biological species concept, stating that "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups." Although various other valid descriptions of a species have been proposed, this concept of reproductive isolation remains the most widely recognized approach to the issue.

1942. Working on his doctoral thesis in zoology, graduate student Raymond Lindeman studies Cedar Creek Bog, a senescent lake on the Anoka Sand Plain of east central Minnesota. He describes the area in a paper entitled "The Trophic-Dynamic Aspect of Ecology" (published after his death at age 27). Lindeman classifies the organisms into trophic (feeding) levels and then determines the energy flows between these levels. His trophic-dynamic model establishes the "bottom-up" perspective as the dominant paradigm for a generation of ecologists.

1943. Agronomist Norman Borlaug joins a program funded by the Rockefeller Foundation to help farmers in Mexico increase their wheat production. This program will develop high-yield, disease-resistant crops and eventually lead to the improved agricultural practices of the Green Revolution of the 1960s and 1970s.

1944. Based on experiments with bacteria, Oswald T. Avery and colleagues establish that the nucleic acid DNA is the essential material that carries genetic properties in virtually all living organisms. This is considered the foundation of modern DNA research, although it would remain for Watson and Crick to describe the structure of the DNA molecule.

1945. David Lack reports that beak size for Darwin's finches in the Galápagos islands depends on whether or not a given species co-occurs with other finch species. In 1959 G. Evelyn Hutchinson concludes that such differences in size evolve to allow different species to partition the food web structure even though their ecological requirements are the same. This issue of body size ratios in co-occurring species becomes one of the classic tests of competition theory

1945. P. H. Leslie develops the Leslie matrix model, which combines the mortality and fertility functions of a population in a single expression. This becomes one of the most widely used tools to determine the increase or decrease of a population over time, as well as the age distribution within the population.

ca. 1947. In one of the most noted examples of an invasive species, the predatory tree snake *Boiga irregularis* is accidentally introduced on the island of Guam. Having neither competitors nor predators on the island, it soon becomes the top predator there. It will be responsible for a severe decline in Guam's native bird population and the presumed extinction of at least 10 bird species, as well as having major impacts on lizard and bat populations.

1949. *A Sand County Almanac,* a collection of essays by naturalist Aldo Leopold, is published a year after the author's death. It brings about widespread public appreciation of the value of biodiversity for its own sake and is considered a founding work of environmental ethics. The book arguably ranks second only to Rachel Carson's *Silent Spring* in terms of its influence on the popular environmental movement.

1949. Wolves appear on Isle Royal in Lake Superior, where the moose population had lived free of predation since first

reaching the island about 1900. This establishes a predator–prey relationship that will be extensively studied by ecologists over the ensuing decades, as they monitor the size of the wolf and moose populations, their interactions with each other, and the effects of relative population size on the island's vegetation.

1951. Studies of plant communities by Robert Whittaker and John Curtis lead to a challenge to the concept of rigid plant associations advocated by Frederic Clements. Whittaker presents the theory and technique of gradient analysis to describe continuous distributions of species along environmental gradients, thus supporting Henry Gleason's contrasting concept of individualistic communities.

1951. To account for the fact that, just by chance, a species may be absent from a site where it would have thrived, John G. Skellam develops the reaction–diffusion model of invasion biology. Skellam's mode describes the dynamics of a population that is both growing and spreading, and it predicts that the front of an invasion will move at a constant velocity.

1952. Ernst Mayr describes what is termed the "founder effect," an instance in which a new population is established by a relatively small number of individuals with limited genetic variation. Such effects are particularly important on islands where organisms arrive from other sites, as by wind or wave action.

1953. Eugene P. Odum publishes the comprehensive work *Fundamentals of Ecology,* along with his brother Howard. This is recognized as the first textbook to examine ecology from a holistic, macroscopic perspective. It uses a "top-down" approach starting at the ecosystem level and describes community stability as being based on the sharing of energy throughout the food web.

1953. James Watson of the United States and Francis Crick of Britain present an accurate model of the double-helix structure of the DNA molecule. This leads to a revolution in the science of biology, in particular the advancement of the field of molecular biology.

1955. The concept of Maximum Sustained Yield (MSY) is adopted as the goal of international fisheries management at a conference sponsored by the United Nations. MSY is the maximum long-term average catch that can be removed from a fish population on a sustainable basis.

1956. Lotka's 1925 work *Elements of Physical Biology* gains a new audience when it is reissued as *Elements of Mathematical Biology*. This book contains the theoretical basis for much of modern ecology, as it covers issues such as evolutionary change, biogeochemical cycles, growth and reproduction, interspecies equilibrium, energy balance, the operations of the senses, and the function of consciousness.

1957. Howard T. (Tom) Odum measures primary production in a number of freshwater spring communities of Florida. He characterizes the transfer of carbon between trophic levels with the goal of understanding how energy moves through an ecosystem.

1958. Charles Elton publishes *The Ecology of Invasions by Animals and Plants,* which becomes the classic text of invasion biology. He concludes that simplified food webs such as monocultures seem to be more vulnerable to invaders than complex ones, probably because they offer greater opportunity to establish new niches. This implies that greater biodiversity tends to produce greater stability,

1958. The oceanographer Charles Keeling begins his decades-long record of Earth's atmospheric carbon dioxide concentrations, as measured at Mauna Loa, Hawaii, and other locations. He becomes the first to confirm definitively the rise of atmospheric carbon dioxide by means of a data set now known as the "Keeling Curve."

1958–1959. G. Evelyn Hutchinson refines and popularizes the concept of the niche, the multidimensional space of resources (light, nutrients, structure, etc.) that is available to and specifically used by a species. He formulates the ecological niche as a quantitative description of the range of environmental conditions that allow a population to persist in a given location, i.e., to have a positive or at least zero (break-even) growth rate.

1959. Crawford Stanley Holling of Canada introduces the concept of functional response, which describes the relationship between prey density in a certain area and the amount of prey consumed by each predator in that area. This will become an important principle of modern population ecology. Holling will also make important contributions to chaos theory and to the development of the field of ecological economics.

1960. Nelson G. Hairston, Frederick E. Smith, and Lawrence B. Slobodkin argue that predators protect the "green world" from herbivores such as rabbits by restricting their densities to levels that allow plant life to flourish. This "HSS hypothesis" provides a top-down alternative to the bottom-up paradigm that fertility is the key to understanding plant biomass. Robert T. Paine later uses the term *trophic cascade* to describe this indirect effect of predation on vegetation.

1960s. F. Herbert Bormann, Eugene E. Likens, Robert S. Pierce, and Noye Johnson serve as the core of the Hubbard Brook Ecosystem Study group for ecological and biogeochemical research in the White Mountain National Forest of New Hampshire. The group makes important contributions in areas such as nutrient cycling, biomass measurement, forest management, and anthropomorphic environmental disruptions.

1960s. The modern field of ethology (innate animal behavior) is established, mainly through the work of Konrad Lorenz, Niko Tinbergen, and Karl von Frisch. A fundamental principle of the field is that behavior has an evolutionary basis. Thus, there is interest in behaviors that seem disadvantageous to the individual performing them; e.g., warning behavior.

1962. Frank W. Preston publishes the last of his three major papers on the mathematical characteristics of ecological commonness and rarity. He points out a consistent relationship between the commonness and rarity of individuals and species in many forms of life, which in his view can be best represented by a lognormal curve.

1962. The naturalist author Rachel Carson publishes *Silent Spring,* an account of the harmful effect on wildlife of pesticides such as the insecticide DDT. The book height-

ens public awareness of the extent to which the natural environment is vulnerable to human intervention. It becomes a best seller and is generally credited with launching the modern U.S. environmental movement at the popular level. In 1972 the use of DDT will be generally banned in the United States.

1963. Harold Barnett and Chandler Morse provide the first empirical analysis of the historic supply of natural resources in the United States. It shows that from 1890 to 1957 the cost in capital and work hours of resources such as timber, fish, minerals, and fuels declined significantly, which is attributed to increased efficiency. This is used by some to argue that the only real limitation on resource exploitation is human ingenuity, not physical supply.

1963. Stanley C. Wecker and Peter H. Klopfer study the question of how a species chooses the place it inhabits. They conclude that this choice is partly genetic, having evolved as a means for detecting the most favorable environment for survival, but also partly physiological/experiential, e.g., affected by the natal habitat or the nature of parenting. Later workers will develop the ideal free distribution model (IFD) to predict the area that an animal will select.

1963–1964. William D. Hamilton proposes a method of accounting for the evolution of apparently altruistic behavior (actions beneficial to the recipient but detrimental to the actor). According to Hamilton's Rule, a behavior that lowers the chance for survival of the individual may occur when it increases the chance for survival of close relatives with similar genetic makeup.

1964. Paul R. Ehrlich and Peter H. Raven collaborate on "Butterflies and Plants: A Study in Coevolution." This popularizes the use of the term *coevolution* to describe a pattern in which reciprocal evolutionary change occurs in two interacting species.

1966. George C. Williams challenges the idea of group selection, the concept that behaviors detrimental to an individual can evolve because they benefit the group. He argues that most seemingly group-selected traits really are advantageous to the individuals performing them. The intuitive basis for this is that if an individual feature were indeed good only for the group, it could not evolve because the individual performers would all die out.

1967. In his studies of the blue-gray gnatcatcher (*Polioptila caerulea*), Richard B. Root employs the term *guild*. He defines this as "a group of species that exploit the same class of environmental resources in a similar way" (in this case, foliage-gleaning insectivorous birds). The concept derives from the medieval practice of the artisans in a particular industry forming a guild to promote their mutual interests.

1967. Lynn Townsend White Jr. recommends that St. Francis of Assisi be made the patron saint of ecology, stating "He proposed what he thought was an alternative Christian view of nature and man's relation to it; he tried to substitute the idea of the equality of all creatures, including man, for the idea of man's limitless rule of creation."

1967. Robert MacArthur and Edward O. Wilson present the theory of island biogeography, an equilibrium theory designed to predict the number of species that will exist on a given island. They propose that the number of species on any island reflects a balance between the rate at which new species immigrate to colonize it and the rate at which established species become locally extinct. An "island" in this context is not only a body of land surrounded by water but can be any insular area, such as a formerly continuous natural habitat now fragmented by encroaching civilization.

1968. Garrett Hardin publishes an essay entitled "The Tragedy of the Commons." He argues that "Freedom in a commons brings ruin to all." That is, if a society allows unregulated use of public resources, the inevitable result will be depletion of the resources, because each individual actor will behave in his own best interest and exploit the commons.

1968. Motoo Kimura of Japan introduces the neutral theory of molecular evolution, which assumes that genetic variation results from a combination of mutation-generating variation and genetic drift eliminating it. The theory is called neutral because allele and genotype differences at a gene are selectively neutral (or nearly so) with respect to each other.

1969. Richard Levins employs the term *metapopulation* to describe an assemblage of local populations living in a network of habitat patches. The Levins model presents the essence of the metapopulation concept, i.e., that a species may persist in a balance between stochastic local extinctions and recolonization of currently unoccupied patches. Metapopulation theory will be further developed by Ilkka Hanski from the 1980s onward.

1969. Robert Paine describes the role that a Pacific Northwest starfish and a large snail from Australia's Great Barrier Reef play in their respective ecosystems. He notes that removal of these two predator species would cause a population explosion of certain of their prey, with severe consequences for the rest of the ecosystem. He borrows a term from architecture to designate such an organism as the *keystone species* for its ecosystem.

1972. Daniel B. Botkin and colleagues present a so-called gap model for forest growth, based on the growth of the individual trees that make up the forest stand. The concept of a "gap" is based on the idea that the death of a large tree creates a space in the forest canopy in which certain species then become established. In the 1980s Herman H. Shugart and others will provide additional gap models.

1972. In "Acid Rain," Gene Likens and colleagues describe the long-term effects of acid precipitation, based on observations at Hubbard Brook, New Hampshire. The report demonstrates an explicit link between the use of fossil fuels in North America and increased acidification of rain and snow. This is consistent with the first description of acid rain, made exactly 100 years earlier by Robert Angus Smith.

1972. John Maynard Smith introduces the concept of an evolutionarily stable strategy (ESS), defined as a strategy so effective that it cannot be displaced by a rare new (mutant) strategy if it has become fixed in a population. He bases this on game theory, reasoning that a population

will resist the development of new traits or behaviors because this may decrease the likelihood of successful reproduction.

1972. Robert MacArthur summarizes his views in *Geographical Ecology: Patterns in the Distribution of Species.* The book's theme is that "the structure of the environment, the morphology of the species, the economics of species behavior, and the dynamics of population changes are the four essential ingredients of all interesting biogeographic patterns." Although he acknowledges the role of history in shaping species assemblages, MacArthur regards useful patterns of species diversity as the result of repeatable phenomena, not chance events.

1973. Leigh Van Valen proposes the Red Queen Hypothesis, referencing an episode in *Alice in Wonderland* in which the Red Queen tells Alice that "It takes all the running you can do to keep in the same place." The analogy is that a species may have to evolve continuously in order to maintain fitness relative to the evolving species with which it interacts.

1973. With "Resilience and Stability of Ecological Systems," Holling initiates interest in the phenomenon of resilience. He describes resilient systems as those that tend to maintain, or restore, their integrity when subject to disturbance or rapid change. The concept of resilience thus becomes influential not only in population and community ecology but also in disparate fields such as systems theory, social science, and economics.

1974. Simon A. Levin publishes two articles (one with Paine) providing the theoretical foundations for the fields of spatial ecology and patch dynamics. Two decades later, in a paper that becomes the most-cited work in ecology in the 1990s, Levin will argue that "the problem of pattern and scale is the central problem in ecology." He perceives the biosphere as a complex adaptive system with patterns of regularity emerging from self-organizing processes; this contrasts with the "Gaiaesque" view of the Earth as a unified superorganism.

1976. Hal Caswell develops the neutral theory of biodiversity, based on the idea that the importance of biotic factors such as competition and predation can be assessed by comparing their empirical patterns with the results of a stochastic model that does not assume their existence. This approach will later be expanded by Stephen Hubbell.

1976. Robert May publishes an influential review for *Nature* entitled "Simple Mathematical Models with Very Complicated Dynamics." May applies chaos theory to mathematical ecology, stating that simple nonlinear equations describing the growth of biological populations can exhibit a wide spectrum of dynamic behavior.

1977. Harold Mooney provides evidence for the theory of convergent evolution, which maintains that different species in widely separated ecosystems, but with comparable climates, will develop similar ways of adapting to their environment. He also takes an economic approach to plant evolution, showing how plants strive to obtain the greatest effect from resources with the lowest expenditure of energy.

1978. Mark L. Shaffer analyzes the Yellowstone grizzly bear population and uses computer simulations to estimate the numbers of bears needed to ensure a reasonable chance of persistence over the next century. This marks the emergence of population viability analysis (PVA), a process of identifying the threats faced by a species and evaluating the likelihood that the species will persist for a given time into the future.

1980. The U.S. National Science Foundation establishes the Long-Term Ecological Research Program, with an initial set of six research sites. LTER's mission is to provide knowledge to protect and manage ecosystems, their biodiversity, and the services they provide. Other large-scale research programs are subsequently created with similar aims of developing ecological knowledge and disseminating it to policy makers and the general public. These include the International Geosphere–Biosphere Programme (1987), DIVERSITAS (1991), and the Sustainable Biosphere Initiative (1992).

1982. David Tilman begins an ongoing study of a series of grassland plots at Cedar Creek, Minnesota. Over time this will yield valuable insights into such issues as plant competition and the relationship of biodiversity to ecosystem function, and Tilman's papers will be among the most cited of any contemporary researcher in ecology/environment. Other highly cited authors of this era include John Lawton (population dynamics), Peter Vitousek (forest ecosystems), and Kevin Jones (environmental contaminants).

late 1980s. The world's marine fisheries catch reaches a historic peak, as newly exploited areas are no longer able to compensate for the decline of traditional fishing grounds. Northern cod, once so abundant they constituted the major source of protein for much of Western Europe, are now severely depleted through overfishing.

1988. E. O. Wilson edits the volume *Biodiversity,* which calls attention to the rapidly accelerating loss of plant and animal species as a result of increasing human population pressure and the demands of economic development. This concept of "biological diversity" had been developing since the nineteenth century, but it is this publication that establishes *biodiversity* as the correct term for the variety of organismal life in a given system of reference at all levels of organization.

1988. Norman Myers uses the term *hot spots* to describe areas of the world that have the combined qualities of high levels of species endemism and high rates of depletion of vegetative cover. He identifies certain tropical forests that meet these criteria and argues that conservation efforts should be prioritized to focus on these areas because the risk of extinction is greatest there and the potential payoff from conservation is the highest.

1988. The Intergovernmental Panel on Climate Change (IPCC) is formed; it will become the leading scientific authority on this issue. In a series of reports (1995, 2001, 2007), the IPCC will state in progressively stronger language that a warming trend has been occurring since the mid-twentieth century and that this trend is directly tied to human activity, specifically increases in greenhouse gas emissions.

1989. James H. Brown and Brian A. Maurer formally introduce the research program known as macroecology,

the study of how species divide resources (energy) and space at large spatial and temporal scales. Reportedly the first use of the word *macroecology* was in a 1971 monograph by the Venezuelan researchers Guillermo Sarmiento and Maximina Monasterio.

1992. General concern about the impact of anthropogenic biodiversity loss is voiced at the Rio de Janeiro Earth Summit. The Convention on Biological Diversity (CBD) is then founded to promote sustainable development and the protection of biodiversity. This leads to an intensified effort by ecologists to understand the effects that changes in biodiversity can have on ecosystem functioning and the likely significance of such changes for humankind.

1992. Roy Anderson and Robert May publish *Infectious Diseases of Humans*, which will become the key reference in the field of ecological epidemiology. This book summarizes the authors' work of the 1970s and 1980s in pioneering the use of mathematical models for studying the movement of infectious diseases through populations and the effect of programs of immunization and control to combat them.