RECOMMENDED READING

TIMOTHY F. H. ALLEN AND THOMAS W. HOEKSTRA. *Toward a Unified Ecology.* Columbia University Press, New York. 1992.

The organization and content of Allan and Hoekstra's text inspired the organization of the text you are now reading.

CHARLES ELTON. *Animal Ecology.* Sidgwick & Jackson, London. 1927.

This excellent classical text reads quickly and contains many modern ecological concepts in seed form.

NORMAN HAIRSTON. *Experiments in Ecology.* Cambridge University Press. 1997.

An important book that complements many of the things addressed in this chapter.

RAY HILBORN AND MARC MANGEL. *The Ecological Detective: Confronting Models with Data.* Princeton, New Jersey. 1997.

An excellent introduction to quantitative techniques in ecological modeling.

STEWARD T. PICKETT, JUREK KOLASA AND CLIVE G. JONES. *Ecological Understanding.* Academic Press, San Diego, California. 1994.

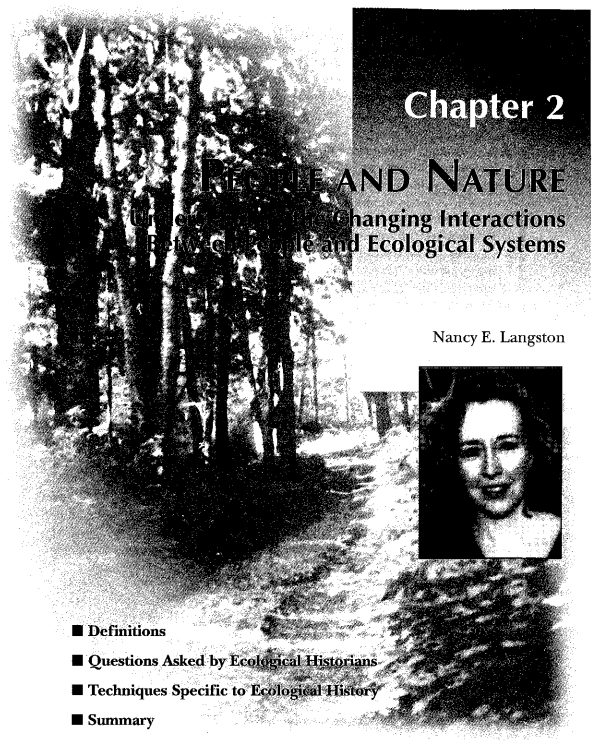
This book provides further background on the current state of ecology.

ROBERT C. STAUFFER. "Haeckel, Darwin, and Ecology." *Quarterly Review of Biology* 32:138-144. 1957.

This short article presents the early history of ecology.

EUGEN WARMING. *Oecology of Plants.* Oxford University Press, London. 1927.

This book gives a good idea of the state of plant ecology in the early part of this century.



Chapter 2

PEOPLE AND NATURE

Understanding the Changing Interactions Between People and Ecological Systems

Nancy E. Langston

- Definitions
- Questions Asked by Ecological Historians
- Techniques Specific to Ecological History
- Summary

A new day has begun on the crane marsh. A sense of time lies thick and heavy on such a place. Yearly since the ice age it has awakened each spring to the clangor of cranes. The peat layers that comprise the bog are laid down in the basin of an ancient lake. The cranes stand, as it were, upon the sodden pages of their own history.
—Aldo Leopold

DEFINITIONS

Environmental history examines the history of human interactions with the non-human world. All environments change, and people have been important forces shaping these changes for only a tiny fraction of Earth's history. In the last ten thousand years, however, human effects on ecological systems have often overwhelmed the ability of these systems to respond to change. This chapter will explore the study of environmental change, asking what the interactions between people and nature mean for the study of ecology.

QUESTIONS ASKED BY ECOLOGICAL HISTORIANS

Why consider humans in an ecology textbook? Isn't ecology supposed to be about natural systems, not about people? The first answer is simple: the world is dramatically affected by humans. Understanding how ecological systems function requires understanding the history of those systems. Changes caused by humans have been—and will continue to be—an important part of that history.

The second major reason to pay attention to humans is that the relationship between science and culture is more complex than most people imagine, and understanding the links between the two helps bring into focus the controversies in modern ecology. Ecology is not only a set of facts, but also a set of questions that people ask about the world. Ecologists have particular worldviews that lead them to ask particular kinds of questions, and therefore know the world in certain ways. Understanding these questions, and the different ways people have answered them, requires knowledge of the relationships between cultural factors and scientific hypotheses. Although good scientists test hypotheses without thought of political gain, the ways scientists formulate their hypotheses reflect their own cultural perspectives, as well as the natural world the scientists study.

Finally, scientists need ecological historians to help answer a question which is not purely scientific, but nevertheless motivates many ecologists in their work: why is the Earth in a state of global environmental crisis, and what should be done about it? For example, ecologists can trace numerous ways that extensive deforestation affects forests, but ecological theory alone cannot explain why people cut the trees (Plate 2.1). The most important causes of ecological degradation lie in human culture, and so understanding the links between culture, economics, and ecology can help devise better strategies for conserving and restoring nature.

Environments Shaped by People

How does a forest, a grassland, a wetland, or an estuary come to work the way it does? Exploring these questions means paying attention not just to current interactions between individuals, species, or energy flows, but also to the history of that system. Any ecological system, no matter how you define its boundaries, is a product of all the events, processes, and **disturbances** that led to its current state.

Ecologists long assumed that they could study the laws of nature apart from human history. Human-influenced systems seemed to be aberrations, because human history seemed too brief in evolutionary time to worry about. Most ecologists believed that over time, natural processes would eventually erase the effects of different initial stages in the life of an ecosystem (Christensen 1989). But recent research shows that past environmental conditions play a continuing role in most ecological systems: you cannot erase or ignore history, and people are one of many sources of historical disturbances that shape environments.

The modern world—no matter how much like a wilderness it may appear—has been measurably altered by humans. Human activities affect the entire globe from the depths

Figure 2.1. The ecology of Australia's bush has been shaped both by ecological processes and by thousands of years of management and intensive cultural interaction by aboriginal peoples.

of the ocean to the highest levels of the atmosphere. Many places on Earth that we view as pristine—the Wyoming wilderness, the Australian bush, the Brazilian rain forest—are actually the results of long interactions between people and place.

The Amazon rain forest, a place North Americans often envision as an Edenic paradise threatened by slash-and-burn peasant farmers, has actually had an extensive history of management by people who used slash-and-burn farming to shape those landscapes (Simmons 1996; Hecht and Cockburn 1990). Australia's bush (Figure 2.1), seen by European conquerors as a desolate wilderness, also had a complex history of aboriginal management and intensive cultural interaction (Goudie 1994; Simmons 1996). The great treeless moors that cover much of upland Scotland and England (Plate 2.2) are not purely natural, but were shaped by the burning activities of prehistoric hunter-gatherers (Goudie 1994; Simmons 1996). As the environmental historian Donald Worster eloquently argued,

> *Scientists must acknowledge, as many have begun to do, that the nature they describe in their textbooks often seems unreal and contrived to the historian. Typically, it lacks any connection to human history and all its contingencies, accidents, cycles, ideas and social forces. Too often science seems oblivious to the fact that human beings have been interacting with nature over a very long period of time, at least over two million years—some would say four million years—and that what we mean by nature is, to some extent, a product of history (Worster 1996).*

Although people have influenced the entire globe, no ecosystem is entirely an artifact of humans. For all the efforts that people have made to understand, manage, and ultimately control nature, a world of ecological processes and complex interrelationships flourishes outside of our control. To say that places have been "managed" by people means that humans have been only one among many influences on them. Human management, even in the most intensely cultivated tree farm or garden, never completely replaces ecological interactions and constraints.

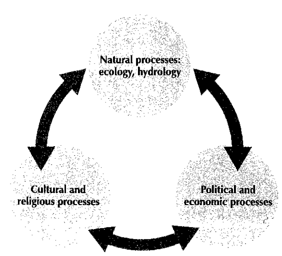


Figure 2.2. The forces driving environmental change include natural processes, but cultural processes (such as ethics, religion, and science), and political and economic processes (including political, technological, and market change) also shape environmental change. Each of these sets of processes in turn affects the other sets, so understanding the links between them is also critical.

Environmental change comes about not just because people cut down trees, plow prairies, or burn fossil fuels, but because they do these things in a world where nature, culture, science, and markets tangle in complex ways. The reasons for environmental change fall into three interwoven categories (Figure 2.2):

- *Cultural:* How did cultural ideals affect the ways different groups of people changed the land? What kinds of visions of the relationship between humans and nature did people bring to the land? Whose vision of the land determined how the land was shaped? In particular, what scientific visions of the forest shaped people's work? In which political and cultural contexts did these scientific theories develop?
- *Political:* Over the course of several centuries, many ecological systems in America and across the globe have been transformed into collections of resources exported out of the region to feed the demands of distant markets. Economics, industrialization, the development of global markets have all had profound effects on the world's ecosystems, and the people who inhabit those ecosystems.
- *Ecological:* What were the biological and physical factors that shaped the landscape? Plant communities, animals, disturbance processes such as fires, floods, insect epidemics, soil processes, nutrient cycles, erosion, and the movement of water are major players in ecological history.

Example 1: Nature and culture on Easter Island

Although many people like to think that all pre-industrial peoples lived in harmony with nature, they were perfectly capable of transforming their environments—often to the point where those environments could not continue to support their cultures. Even in some of the places most remote from industrial civilizations, humans have had profound effects on the places they inhabited. The rise and fall of civilization on Easter Island illustrates some of the ways pre-industrial peoples could alter their environment, and the ways these environmental changes could in turn affect culture (Bush 1997; Ponting 1992).

More than 3,500 km from Chile and 2,200 km from the nearest inhabited land, Easter Island is one of the most isolated islands on earth (Figure 2.3). About 400 AD, Polynesians in enormous dugout canoes found their way to the island, a forested landscape with palm trees, no mammals, and abundant birds. To provide food while at sea, the settlers carried with them a species of rat. When they reached the island, the rats jumped ship and spread throughout Easter Island.

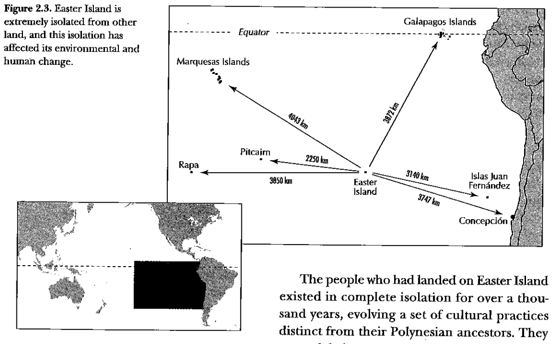


Figure 2.3. Easter Island is extremely isolated from other land, and this isolation has affected its environmental and human change.

Figure 2.4. The enormous statues on Easter Island have long fascinated people who wondered what they meant and how they could have been built.

The people who had landed on Easter Island existed in complete isolation for over a thousand years, evolving a set of cultural practices distinct from their Polynesian ancestors. They revered their ancestors and erected great statues several meters high carved from volcanic rock (Figure 2.4). The population was probably divided into farmers, stonemasons to build the religious statues, and fishers, who provided much of the protein sources.

Archaeologists and paleoecologists (Bahn and Flenley 1992; Flenley and King 1984) recently reconstructed the forest and human history of Easter Island (Figure 2.5), using archaeological records from island caves and pollen records from lake mud. Both sources document the rise and fall of an ecosystem and civilization. When the Polynesians arrived, the island supported a species of palm that provided wood large enough for the construction of seaworthy dugout canoes. These canoes enabled islanders to fish for sharks and large fish and to visit small, uninhabited islands over 400 kilometers away. These islands were home to dense bird colonies, which provided an important protein source to supplement the Easter Islanders' fish catches. The islanders rapidly logged the palms for shipbuilding, and new palms failed to replace them, probably because the escaped rats rapidly multiplied and devoured so many palm nuts that the forest could not regenerate. The pollen records show that for more than 30,000 years before humans arrived, the islands were forested. When the Polynesians arrived, forests began a steady decline, until by the late 1600s, when Europeans arrived, the islands were almost entirely treeless.

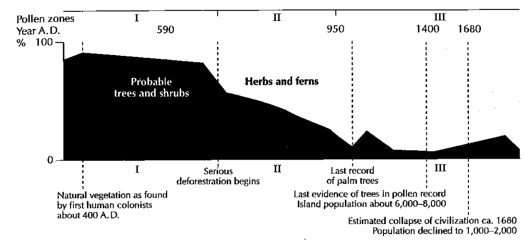


Figure 2.5. The pollen history of Easter Island illustrates how trees began to decline after people arrived on the island. Redrawn from Flenley and King 1984.

Soil erosion followed deforestation, fertility in the fields declined, and farming deteriorated. When the last palms were cut, islanders could no longer build the canoes to get fish from the sea or eggs from the bird colonies. Famine resulted, leading to warfare, cannibalism, a population crash, and finally the end of the Easter Island civilization.

Nothing, unfortunately, is unique about this story. Similar cycles of over-exploitation of resources, deforestation, erosion, famine, warfare, and societal collapse are evident from the archaeological record of many islands. Humans have a long history of transforming their environments, and those transformations may make it impossible for humans, along with many other species, to persist.

Example 2: The Eastern North American forest

While Easter Islanders destroyed their own home and culture through resource over-exploitation, the story is not always so grim. In eastern America, forest exploitation was followed not by ecological and societal collapse, but by recovery.

When English settlers arrived at the Plymouth colony in New England in 1620, they thought they were stepping into what one observer called,

> *...a hideous & desolate wilderness, full of wild beasts & wild men... The whole country, full of woods & thickets, represented a wild & savage hue.*
>
> —*William Bradford, 1620*

The settlers thought they were gazing upon a desolate wilderness unaltered by people, but actually the forests of eastern America had a long history of human transformations. Although the northern forest had never been clearcut or extensively logged, Native American practices had radically affected its development, as William Cronon (1983) and William Denevan (1992) have shown. Native Americans moved into the northern forest soon after the retreat of the glaciers 11,000 years ago. Soon after their arrival, huge Pleistocene-era mammals such as mammoths, mastodons, armadillos, ground sloths, giant beavers, dire wolves, and saber-toothed tigers went extinct (Figure 2.6). Scientists debate whether Native American hunting, climate change, disease, or a combination of all three destroyed the animals. Whether or not Native Americans were responsible for the demise of the huge mammals, they soon altered the forest, clearing plots of land for shifting agriculture, and burning forests in patches to keep them open, parklike, and full of berries. These burns created excellent habitat for deer and other wildlife, and likely increased deer populations (Cronon 1983). The tribes were mobile, allowing farm plots to regenerate back into forest and giving soils time to recover from cultivation.

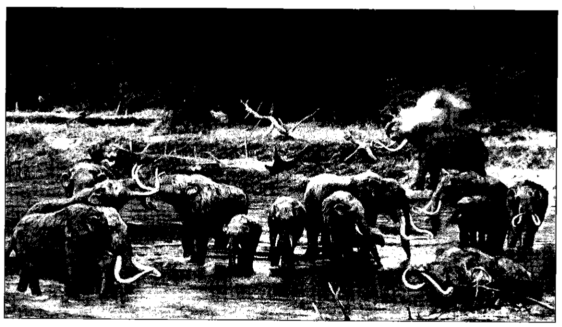


Figure 2.6. Soon after the arrival of people to North America, most of the huge Pleistocene-era mammals such as the mastodons illustrated here went extinct.

Europeans introduced an economy which rested not on hunting and shifting cultivation, but on the extraction of four primary resources: timber, furs, fish, and agricultural products. Settlers exported timber to Europe and cleared large plots of forest land for settled agriculture (Cronon 1983; Merchant 1993; McKibben 1996; Whitney 1994). Although Native American farm plots had quickly recycled back into forest cover, the demands of colonial property ownership required that farm plots remain fixed on the landscape. The effects on soil fertility and erosion were often dramatic. Forest cover across the Northeast dropped from 70 percent to 25 percent or less (Figure 2.7). As the trees ran out, loggers moved from New England to New York, Pennsylvania, the Great Lakes, the South, and eventually to the forests of the West. As soil fertility declined, agriculture left the region as well.

What can we learn from this contrast between Native Americans and Euro-Americans in the eastern forest? Both groups affected the forests they lived within, but Native Americans extracted resources without depleting the resource base their cultures depended upon. Europeans had effects that were much more dramatic in the short term, for they, like the Easter Islanders, extracted resources too quickly to sustain their own economies. Yet the outcome was very different than on Easter Island. While Easter Island's forests have never

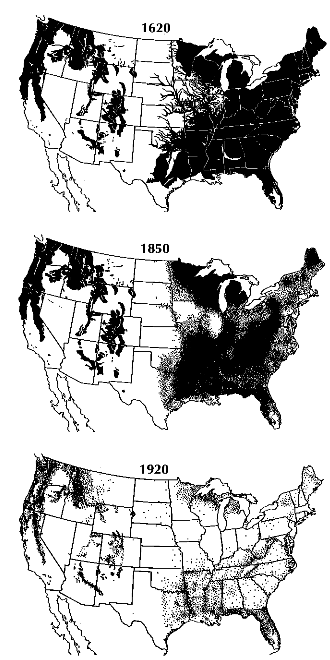


Figure 2.7. The extent of unlogged forest across North America declined with the spread of Euro-Americans, beginning with the logging of the New England forests. Each dot represents 25,000 acres. Adapted from Greeley 1925.

returned, the landscapes of New England are once again forested; for example, trees now cover nearly 90 percent of Vermont. These recovered forests are not the same as their predecessors: the dominant tree species have shifted, and stands of trees are often smaller and denser, leading to changes in soil conditions, temperature, and water availability (McKibben 1996). Nonetheless, many wild animals that were nearly extirpated from the region in the nineteenth century—including wolves, bear, cougar, and beaver—now reinhabit landscapes where people thought they had vanished for good. As forests come back, they create a new set of ecological relationships, leading to new landscapes and new choices and responsibilities for human management.

Example 3: The Mediterranean

As an example of the ways that cultural, economic, and ecological forces interact to shape the history (and future) of an ecosystem, consider the Mediterranean (McNeill 1992; Hughes 1993). Scholars have argued that one of the three worst environmental disasters in human history happened during the era of the Ancient Greeks in the Mediterranean—at the same time their civilization was constructing the foundations of western rationality and science (Worster 1979; the other two disasters were soil erosion in China around 3,000 B.C. and the Dust Bowl on the American Great Plains in the 1930s).

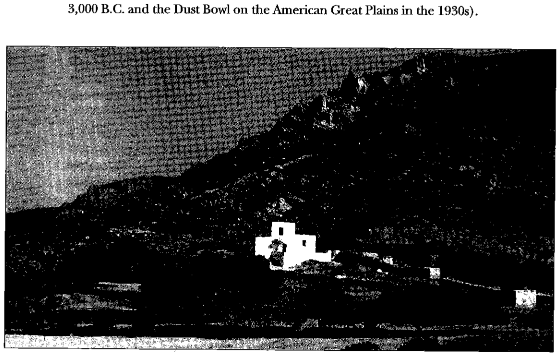


Figure 2.8. The lovely views of bare limestone ridges, such as this scene in the Greek uplands, are in part a product of deforestation caused by centuries of farming, goat grazing, shipbuilding, and logging for mine smelters. From a photo by Johannes Foufopoulos.

When you look at the mountains of the Mediterranean today, (Figure 2.8) you see beautiful landscapes, with bare limestone ridges between which lie picturesque villages. Both the villages and the limestone ridges are lovely, but both are dying. The villages are now empty shells where few but the very old live; the others have gone off to cities to find jobs. Over thousands of years, people have struggled to make a living in these hills, grazing goats, logging trees, planting wheat, fighting battles, hunting wildlife, writing poetry, founding empires, creating much of the philosophy that forms the basis of western culture. In the process, people stripped the hillsides of their trees (hence the lovely views), their soil, and their ability to support much life, human or otherwise. People built empires from the resources extracted from these ecosystems, but in extracting without limit, the empires eventually destroyed themselves from within. To understand why, one needs to understand two interconnected factors usually seen as separate: ecology and economics.

Just after the end of the last ice age, 12,000 years ago, pollen records show that many Mediterranean areas, low elevation and high, supported forests of oaks and pines that have long since dwindled. Focusing on Greece, the geology can be roughly divided into three main zones. The *plains* are low-lying basins filled with silts washed off the hills by erosion—a zone that is readily farmed. At higher elevations are *hills* of volcanic lavas; still higher are *mountains* formed of hard limestone and thin, easily erodible soils (Rackham1990).

Humans have inhabited the Mediterranean basin for at least 500,000 years (McNeill 1992), but populations in the region remained relatively low for most of that time. For about 490,000 years of inhabitation, people were largely on the move, preferring the lowlands to the mountains for gathering resources. They hunted forest-dwelling animals, mostly deer, and burned woodlands as part of their hunt. These fires probably had strong effects on forest development, keeping forests open, free of dense undergrowth, and dominated by species tolerant of fire and intolerant of shade. Fires set by hunters initiated the long process of human-induced erosion, but because people had no livestock grazing in the forests, vegetation recovery after fire was probably rapid (McNeill 1992).

During the Neolithic period (11,000 years before present), the climate became increasingly arid, and many groups of people in the region began to shift from hunting and gathering to agriculture. Early farmers cleared many of the lowland forests for fields, and by 3,000 years ago, the plains of Northern Greece had lost most of their forests. Although the first Greek farmers did remove large swathes of forest, their farming practices seem to have been relatively ecologically stable, for archaeologists have evidence that farmers developed conservation techniques to sustain the soil and nutrients in their fields (Rackham 1990). Farming on steep slopes is hard on the farmer as well as the soil, and most farmers tried to leave hill slopes in forest, or else plant orchards and vineyards (which do not need to be plowed each year, thus reducing labor and erosion). When farmers did have to plant on slopes, they tried to plow on contours and terrace their fields, minimizing soil loss. By spreading lime on the soil, adding animal manure, and planting legumes which fix nitrogen into the soil from the air, farmers may have maintained nutrient cycles in their fields (Rackham 1990).

But farming soon led to an increase in human population, and in search of more land to put into production, people began moving up the hillsides, clearing forests on steeper hills and hard rock soils—places that are slower to recover from disturbance and soil loss. Farmers also introduced livestock, particularly goats, into their forests and farms. Although forests can recover from many disturbances, repeated grazing by goats seems to have overpowered the forests' ability to regenerate on cleared land. Livestock grazing, while providing manure for returning organic matter to farm fields, hastened ecological deterioration on overgrazed pastures and scrublands. Manure was available only part of the year, since during the hot summers, herders brought goats and sheep up to the hill lands. Political boundaries restricted herders to limited pastures, resulting in more overgrazing. Shepherds created more grazing land by burning forests and cutting rings of bark off trees to kill them (girdling). Between 500 B.C. and A.D. 25, many Greek writers such as Herodotus and Aristotle commented on the rapid replacement of forests with pastures and fields, while Plato warned about severe soil erosion and the associated loss of precious water sources (Simmons 1994).

Cultural changes sparked even more rapid ecological changes. The Greek empire that ruled much of the Mediterranean during this era focused on the sea, using their power on the ocean to colonize distant lands. Constructing ships to support this empire required spectacular quantities of timber from a land already losing its forests. Loggers climbed ever higher up into the mountains to find good trees for building ships. Entire forests became ocean fleets. As ship-building technologies developed, the cultures shifted from locally-producing farmers to an empire based on a seagoing civilization and extensive trade. Growing markets for agricultural goods were coupled with increasing specialization of agricultural products. Farmers in different regions focused on either wheat or olives and vines, depending on their local ecology, and this in turn fostered accelerating economic and population growth (McNeill 1992). As mining developed, deforestation accelerated, for the technology of metal smelting demanded ever larger quantities of timber to keep the fires burning. Mining, logging, and farming reduced wildlife habitat, and by 200 BC, the lion and the leopard no longer inhabited Greece; wolves and jackals survived only in the mountains. So much soil eroded that silt began to fill in river deltas and harbors along the Mediterranean Sea, ruining ports that the empire depended upon and creating low-lying swamps, which were perfect habitat for the malarial mosquitoes that plagued city dwellers (Simmons 1994).

How does economics fit into this story? Although as the Easter Island example illustrates, global markets are not a necessary condition for environmental degradation, extensive trade often hastens ecological problems. When resources get siphoned out of a region, maintaining the fertility of the region becomes difficult. Local peasants, farmers, and herders are continually forced to extract more and more simply to survive, and they lose the ability to respond to signs of ecological deterioration. For example, in Mediterranean Spain during the Middle Ages, cooperatives run by large families managed sheep grazing (McNeill, 1992). Grazing made a few people very rich; most people, however, became impoverished. The king supported grazing monopolies, because much of the money went to the crown to support his empire. These grazing monopolies gained a great deal of political power, and the king allowed them to cut any trees they wanted to increase forage for sheep. Instead of keeping sheep in the same low-elevation pastures year round, Spanish shepherds moved them up into the mountains for the summer, where grass and water were more abundant, a practice called **transhumance.** Transhumance was good for the local pastures, for it rested the grasslands enough to allow some recovery from grazing. But transhumance could have dramatic effects on other ecosystems. When shepherds moved their vast herds of sheep hundreds of miles each spring to summer grazing areas, those sheep ate everything along the way (Figure 2.9), infuriating the peasants who lived along the route. Peasants planted trees to try and reduce the erosion from these migrations, but sheepherders cut those trees to replace grasslands that were deteriorating from overgrazing. When peasants protested that their lands were overrun by a plague of sheep, the King had the peasants killed or tossed into jail. Peasants found it increasingly difficult to farm sustainably, since they had to meet the demands of outsiders.

Sustainable use of land requires that the people using the land be able to respond to clues that tell them when ecological conditions are changing. A good shepherd

Figure 2.9. Large bands of sheep, such as this group resting in an Oregon meadow in 1913, could dramatically damage local vegetation. From a photo probably by M. N. Unser, 1913, USDA Forest Service.

learns to read the land, learning that when a certain species of grass gets too short in a field, it is time to move the sheep on, otherwise little forage will return next year. A good farmer also learns to read ecological signs, adding a little more manure or allowing a field to lie fallow when plant growth slows. This sensitivity to changing ecological conditions gives one the ability to respond to the limit of a specific place—a process now called **adaptive management** in resource management circles. Adaptive management becomes impossible when one is forced to meet the demands of outsiders who are not under those ecological constraints, as happened in Mediterranean Spain.

Across much of the Mediterranean, forests did not return after they were cut and grazed; scrubby vegetation took their place. Why did much of the Mediterranean fail to reforest, when many forested landscapes such as the New England forest have recovered well from deforestation? Mediterranean landscapes were less resilient to human activity than New England landscapes for reasons related to geological activity, ecology, climate, and soil. Ecological constraints are often much more severe in semiarid environments such as the Mediterranean than in humid regions such as New England. Greece is also a tectonically active country: the mountains are still rising, and the limestone landscape of the uplands is also quite dynamic; water percolates through the rocks, eroding the mountains from within, leading to landslides, sink holes, caves, and vanishing springs. Erosion is an inherent property of these landscapes, with or without people (Rackham 1990).

Erosion is not always a bad thing—past erosion from the mountains created the fertile soils of the plains—but human activity can accelerate erosion to the degree that plants cannot easily reestablish. People can inadvertently establish **positive feedback cycles,** where an event creates conditions that favor the recurrence of that event, thus leading to rapidly accelerating changes. For example, in the dry climate of the Mediterranean, when erosion, grazing, farming, or drought led to a decline in vegetation, that decline created conditions that made future declines in vegetation more frequent and more intense. Tree roots on steep slopes in Greece had held onto the soil; when plows and goats destroyed those roots, new trees had difficulty regenerating, so fewer roots existed to hold onto soil, and more soil eroded off, leading to fewer roots, more erosion, and so forth, until much of the soil was in the sea instead of on the hills. As the soil declined, so too did the quality of fodder for animals. Since animals were in poor condition, people had to graze more and more of them to survive, further damaging what soil was left. The resulting positive feedback cycles seemed to have pushed many Mediterranean ecosystems over a threshold where forests could not recover for thousands of years.

The science of ecology has its roots in these Mediterranean ecosystems, for it was here that western science has its philosophical origins. You are studying this book because of a civilization that once flourished in an fragile, dry landscape. When the ecosystems supporting it were depleted, the civilization collapsed, but the habits of thought that flourished there have remained fundamental to western science. Ironically, the culture of science has long been an important factor contributing to environmental degradation, but science also offers some of the best tools for reversing that degradation.

Example 4: Beaver and models of nature

Global markets for goods, such as those that developed in the Mediterranean, concentrate demand on a small, distant producing area, often overwhelming the ability of that area to extract resources. This can have cascading effects not just on the resource extracted, but on the entire ecosystem, as the removal of beaver from the Rocky Mountain West illustrates. In the nineteenth century, the European fashion of beaver hats transformed ecosystems halfway across the globe. When Europeans arrived in North America, between 60 and 400 million beavers ranged over about 6 million square miles of varied habitats on the boundary between water and land, from Arctic tundra down to the deserts of Northern Mexico (Naiman et al. 1986, Naiman 1988). Beavers still occupied nearly every body of water when fur trappers began to work the mountain waters in the early nineteenth century. Within just thirty years the beaver had nearly vanished.

To understand the ecological effects of removing beaver from the landscape, consider first what beavers did to the ecosystem. They cut down trees and built dams—as many as 15 to 25 dams per mile of creek in prime habitat—and those dams had wide-ranging effects on the landscape (Plate 2.3). Dams slowed the water flow, and by creating wetlands, they buffered floods and helped prolong the late summer flow of streams—both critical factors in allowing dry forests to persist. The dams retained tremendous amounts of sediment and organic matter in the stream channel (a single dam could gather 6500 cubic meters of sediment behind it), and this too had critical effects on the streams as well as the surrounding forests. The great heaps of sediment provided a massive reservoir of carbon—20 times the carbon in free-flowing stream sections—and this buffered nutrient flows, because the sediment piles released carbon more slowly than surrounding areas. Flooding the soil increased the amount of nitrogen accessible to plants, so beaver activity enhanced nitrogen availability across the landscape. Because many mountain forests are nitrogen-limited, beavers may have indirectly increased forest productivity (Naiman 1988).

Beavers also shaped the direction of forest history. When they toppled trees, they were not indiscriminate clear cutters. They favored certain trees and shrubs and ignored others, so eventually the less-preferred trees came to dominate the forest along the streams. If beavers cut down enough of the trees they liked, they would end up with a forest they could not live in. Then they would have to abandon that stream reach for a while, until their favored trees came back. Should beaver density grow high enough, it might virtually eliminate preferred hardwood species, thus creating patches of bright light in the riparian areas where shrubs could come in thickly. The effect of all this cutting and moving about was an increase in diversity along the streams (Naiman et al. 1986; Naiman 1988).

Beavers preferred smaller streams because spring floods would knock out their dams in larger streams. Yet their effects were not limited to the small streams they dammed. Beaver-cut wood from upstream dams swept into bigger streams, adding large woody debris that formed an integral part of salmon habitat. These logs in turn accumulated debris and sediment, which acted as sources of carbon and nitrogen for the larger streams. Beaver alterations made watersheds more resistant to disturbance, as well as more resilient—quicker to recover from disturbance (Naiman et al. 1986, Naiman, 1988). Beaver modifications rippled across the landscape, and could last for the centuries it might take an abandoned beaver pond to change back to forest.

Removing beaver changed all this—but not in clear or simple ways, since even when beaver vanished, their ponds persisted. **Succession** in abandoned beaver ponds was rarely straightforward. Instead of moving in an orderly fashion from pond to marsh to meadow to forest, regrowth occurred in complex jumps and pauses. Some marshes, bogs, and forested wetlands remained in surprisingly stable condition for a century; others quickly reverted to forest. Beaver ponds in various stages of creation and decay formed a shifting mosaic of diverse patterns across the landscape.

No one at the time of the fur trappers realized that beaver's presence had been instrumental in shaping the landscape. Nearly all the streams that American ecologists have ever studied were streams that trappers had stripped of their prime shapers. The models of nature that stream ecologists have used to formulate their ideas about how "normal" streams function are therefore not normal at all—they grow out of impoverished waters.

What Is the Relation Between Science and Culture?

As the beaver example illustrates, understanding the current ecological functioning of a system requires first examining the human history of that system. To understand ecology, one also has to understand the history of the science itself. Ecology is not merely a collection of details gathered by brave scientists who go off to the Arctic and watch wolves, or who live in the Costa Rican rain forest and study bats. Ecology, like all sciences, reflects a set of views about the world, a set of choices about what is worth observing and measuring. Trying to disassociate ecology from the people asking the questions leads to a skewed view of the science. As the historian of science Peter Bowler put it, science is a process that

> *...mediates between the scientists' creative thinking—stimulated by a host of cultural factors—and their efforts to observe and interpret the external world.*

To understand this, think of a person looking out at the world through a pair of eyeglasses or contact lenses. Everyone views nature through lenses, whether their vision needs correction or not. These lenses are made not of glass or plastic, but instead of cultural beliefs, perceptions, ideas, desires, dreams, ethics, religious ideals, and scientific paradigms. These **cultural lenses** profoundly shape the practice of science and the ways science is used to transform the Earth. Figure 2.10 shows a scientist embedded first within a cultural world and then within a larger natural world. Her perceptions of that natural world are refracted through a set of cultural lenses. Saying that "nature is culturally constructed" does not deny the independence and importance of the larger world. But the scientist cannot know that "real" world directly; what she knows is her perception of it.

Scientific theories are models of nature; they are ways of making sense of the world by reducing complexity to a subset of measurable factors. People create those theories, and those people live within a particular culture and society. For example, during the 1930s and 1940s, a group of ecologists from Chicago led by Warder Allee challenged the contemporary paradigms in community ecology that assumed **competition** structured relationships between organisms. Allee and his fellow ecologists argued that cooperation was more prevalent and important than other ecologists recognized. Historian of science Gregg Mitman (1992) has demonstrated that the Chicago School conceived first of an idealized human society—one where people cooperated rather than competed—

Figure 2.10. A scientist's perceptions of the natural world she is studying are refracted through the lenses of her culture.

and then framed their theories about the ecological world within the context of their ideals for the human world. As this example suggests, ecologists see the world through a set of complex cultural and historical lenses, and those lenses frame the patterns they perceive as significant.

Animal behavior

To make this concept clearer, we turn briefly to animal behavior, looking at a few of the changing ideas about primate social systems. After World War I, when evolution was generally accepted among biologists, many animal behaviorists argued that studies of the primates should throw light on human behavior. Suggesting that some aspects of human behavior might have been shaped by evolution brought biologists into sharp conflict with anthropologists and sociologists, most of whom believed that cultural and social evolution was entirely unconstrained by biology. When primate biologists argued that the behavior of apes was dominated by males within a family group, this only seemed to strengthen the stereotype of male dominance that was the norm for European and American culture at the time. Critics accused biologists of trying to justify cultural inequities with an appeal to nature, arguing that biologists were simply projecting their own prejudices onto the behavior of the animals (Bowler 1993, Haraway 1989).

Early observers studying primates focused on dominance behavior. They developed a set of ideas about dominance structure and hierarchy, based on their observations of fierce alpha males who fought down the other males, ostensibly using physical aggression to keep the group in order. In the 1920s and 1930s, men such as Solly Zuckerman and Robert Yerkes argued that a family group wherein conflict over resources was resolved through aggressive displays (Figure 2.11), and a single powerful male was dominant, was the natural model for primates. Their work was done largely on primates in captivity, and these studies argued that traditional values of male dominance were part of our evolutionary heritage (Bowler 1993).

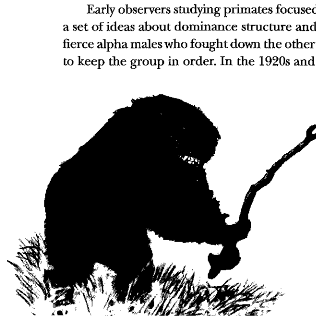


Figure 2.11. Chimpanzee threatening with a stick. The ways that scientists have interpreted the role these aggressive displays play in primate societies have shifted as more women have come into primatology.

Studies of aggression and dominance grew out of the work of early ethologists such as Konrad Lorenz, who won a Nobel Prize for his work on animal behavior. Lorenz saw dominance hierarchies as an image of the ideal state, with a dominant male leader (the alpha male) keeping lower-ranking animals in line, and the interests of individuals subsumed to interests of the group or the state. To a certain degree, early ethologists were projecting their own ideals of culture onto the animals when they focused on aggressive interactions between males: Lorenz came out of a long European cultural tradition that valued dominance and hierarchy in human society, and therefore tended to focus on it in the rest of nature. Male primates, particularly the baboons on which much of the early work was done, can certainly be aggressive, so those observations were not incorrect. Yet people interpret their observations, and culture influences scientists' interpretations. With primates, the hypothesis that aggressive interactions formed the basis of primate society was a hypothesis deeply shaped by cultural assumptions.

Scientists tended to ignore what female primates were doing, and so overlooked the importance of female coalitions and mother-child relationships within the groups. The focus changed when more women came into the field and began observing females, looking at the roles of communication, coalition building and sex in structuring social interactions (Altmann 1980). For example, Jane Goodall and Dian Fossey were the first women to do formal research on primates in the wild, Goodall focusing on chimpanzees and Fossey on gorillas. In her early work, Goodall argued that chimps were peaceful, loving, tool-using vegetarians. Fossey likewise rejected the idea of gorillas as savage killers, claiming that they were gentle creatures. Yet later research by Goodall showed that chimps engaged in hunting, group violence, and cannibalism (Goodall 1986). Goodall was devastated by these results, for they overturned her hopes that gentle, loving cooperation was the "natural" primate social structure, and that brutal warfare was only a recent human innovation that was not part of true primate nature. If violence, warfare, and cannibalism were natural to chimps, what did that say about human society?

Primate studies clearly offer a number of models of what might be "natural" in humans. Some primatologists argue that male dominance is built into all primates; others argue that interactions between females and children structure primate society, and that male dominance means little except to other, mid-ranking males. The ways scientists see the world are shaped by their expectations and their cultural history. These cultural lenses do not mean early ethologists were doing bad science. Lorenz transformed and energized the study of animal behavior with his work on aggression; the early work on primates in captivity provided the groundwork for later field work. But people do science. The ways scientists have looked at primates reflects something about primates, but also a great deal about people, and people's relationship to nature and science.

Ecology, like all sciences, is affected by the cultures and ideologies of the people who study it. The complexity of the world is difficult for humans to imagine—there are millions of behaviors an ethologist could observe, measure, respond to at any moment. Science, like all human activity, is a way of making sense of that bewildering complexity by choosing what to notice and what to filter out and ignore. No one can process every single thing happening. Problems only arise when scientists deny that they have cultural biases, and that what they see may not be all there is to see.

How Have Ecologists Viewed Nature? History of the Balance of Nature Concept

Over millennia, human views of nature have shifted in ways that reflect changing cultural assumptions about the human role on Earth, and those views in turn change the ways people transform the Earth. To explore this dialectic between scientific ideas, culture, and ecology, we will examine changes in the concept of the balance of nature.

Figure 2.12 shows a stand of old-growth forest (forest that has never been logged). Along with many large, mature trees, in such a forest one might see a few deer, tracks left by a wolf pack, some young trees, *understory vegetation*—the plants beneath the trees—and a small opening. Such a picture suggests many questions:

- Will a forest still be there in 100 years?
- Will a fire or insect epidemic kill the trees?
- When the old trees die, will they be replaced with the same species, with other tree species, or with no trees at all?
- Will the opening get bigger or fill in with trees?
- Will deer multiply and destroy the understory vegetation?
- Will a wolf pack eat all the deer and then starve to death when their food is gone?

Figure 2.12. Old growth forest, looking out onto a sunny opening. From a photo by Nancy Langston.

Over thousands of years, people have looked at forests like these and asked similar questions. In the last several decades, however, what scientists believe to be the answers have changed dramatically, for a revolution has occurred in the worldview of ecologists. Instead of seeing a world in balance, most ecologists see a world of flux and uncertainty.

Until recently, most ecologists would have looked at this old-growth forest and believed that it was in stable **equilibrium** with its environment, meaning that dead trees were replaced with the equivalent biomass of young trees. A young forest, they believed, developed over time to attain a constant and predictable endstate, the **climax community,** which in some ways resembled an organism. Just as you would expect a puppy to develop into a dog instead of a chicken or a cucumber, ecologists predicted that a young forest would eventually develop into a specific climax forest community. If a disturbance such as defoliating insects entered the forest, they might interrupt the forest's development toward climax, but scientists believed "...this was a transitory state, a foreign intrusion into an otherwise balanced and unchanging community that in the healthy ecosystem was quickly 'disposed of' in the same sense a healthy organism disposes of disease" (Perry 1995). In other words, ecologists believed in the **balance of nature**.

What exactly the balance of nature means to people has changed over the centuries, as the following sections will describe, but underlying most beliefs about nature was an assumption that ecosystems were essentially static. Any change would occur in a predictable manner and would lead to a constant endpoint. This was a **deterministic model:** ecologists believed that the direction of change was determined by laws that people could understand (and manipulate, if they were applied-forest ecologists).

These ideas made their way into popular culture, and most people felt "that nature undisturbed displays miraculous order and balance" (Pollan 1992). They hoped that if people only left nature alone, it would tend toward a "healthy and abiding state of equilibrium." In other words, people typically assumed that the forest was ruled by natural law, capable of preserving its balance if only humans could avoid disturbing it. Most people would have assumed that to protect the forest in Figure 2.12, one simply needed to draw a line around it and keep other people out.

Although most non-scientists typically still believe in balance within nature, over the last several decades a revolution has occurred in ecologists' views. Instead of seeing a world of equilibrium and stability when they look at Figure 2.12, the average ecologist now sees a forest marked by flux, instability, and unpredictability. What has changed is not the forest, but the ideas within the scientist's head. In this view of the world, there are no fixed laws tending toward greater balance and stability in nature; chance events are extremely important, so the direction of changes in the young forest would be impossible or difficult to predict. Would trees, shrubs, or grass come into the opening? Hard to say. Would the forest still be there in 100 years? It all depends. Would predators keep herbivores in balance with the habitat? Probably not. These ecologists believe "that the natural world is far more dynamic, changeable, and entangled with human history than popular beliefs about 'the balance of nature' imply" (Pollan 1992). Protecting the forest in Figure 2.12 would mean, to such an ecologist, less emphasis on protecting the structure that is already there, and much more emphasis on the processes both inside and outside the boundaries.

Who is right? Is nature essentially orderly, or is it chaotic and random? Are the living and non-living members of a community linked together into a harmonious, interdependent system? Or are all the inhabitants of a place simply there by chance, blindly striving for the best each one can do on its own? Is that forest essentially a static place, or a place of random, unpredictable changes? There are no single right answers to these questions (and indeed, most current ecologists would argue that the truth probably lies somewhere in between). People have wondered about the balance of nature for thousands of years, and for thousands of years people have searched for order and pattern in nature (Bowler 1993, Egerton 1973, Egerton 1977, McIntosh 1985, Tobey 1981, Takacs 1996, Worster 1994). The next several sections of this chapter will address the ways ideas about the balance of nature have developed in the last two thousand years. At the end of the chapter, two still unresolved questions will be discussed:

- Is the new vision of dynamic nature any closer to the truth about the real world, or is it instead yet another set of models that reflect current cultural assumptions?
- How can these changing models help solve current environmental problems?

Early Theories About Balance in Nature

Greek view of balance

Ancient Greeks certainly recognized the fact of change in the world—in human affairs, in populations of animals and plants, even in climate. But they believed that these changes cycled around a stable point of equilibrium. Seasons came and went and came again, in much of the world. When the winter rains came, spring would eventually return. Food might become scarce for a time, but eventually food returned. The natural world of the Greeks, overall, seemed balanced, even though stability was rarely true for the human world.

Nonetheless, the Greeks occasionally perceived that stability was threatened. A plague of locusts might descend upon the crops and devour the grain. Eventually, however, species numbers usually returned to normal. These observations led to a set of questions: Why did population numbers so often seem stable? And why, when explosions and collapses did arise, did those so often lead, not to complete disaster, but back to stability?

One place people looked for answers was in the regulation of animal numbers (Figure 2.13; see Chapter Seven for much more on **population regulation**). The Ancient Greeks asked a simple question: how can diversity be maintained in a world where some species eat others? The Greek philosophers believed that nature worked not by magic or arbitrary powers, but by laws that human reason could hope to understand. Yet this did not preclude a faith in divine order: they assumed that divine providence was the source of the laws of balance. For example, the Greek philosopher Herodotus believed that natural laws comprehensible to human reason kept predators from driving prey populations to extinction. He argued that differences in reproductive rates maintained numbers of predators well below the available numbers of prey, so that predators would not entirely wipe out prey numbers (Egerton 1973). His explanations of the mechanisms that keep predator reproductive rates low and therefore nature in balance were based on hearsay, rather than on observation of the natural world. For example, he argued that lions (which roamed much of Europe and Mediterranean before human pressure reduced their range) were kept in check by limited fecundity. Herodotus suggested that the mechanism limiting lion reproduction was this: since lions had such sharp claws, each lioness could only have one cub in her life—the cub must rip out its mother's womb while being born. While his mechanism was not religious, Herodotus believed that difference in reproductive rates were ordained to serve a divine purpose—in other words, the gods created predators with low reproductive rates so that balance in the universe would be maintained. Natural history proceeded according to a divine plan. Human history might seem random and uncontrolled, but not nature.

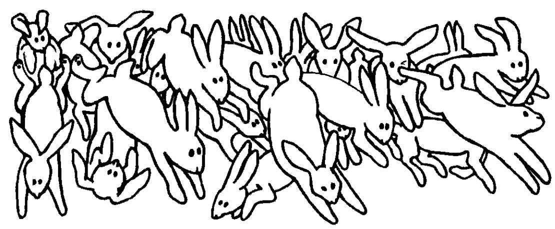


Figure 2.13. For millennia, people have wondered what regulates animal numbers. Populations of animals sometimes explode and overwhelm their habitats.

Christian views

Although the rise of Christianity had profound effects on western cultures, a faith in the balance of nature remained strong. This idea was so fundamental that it became what the historian of science Frank Egerton (1973) called a "background assumption." Rather than trying to analyze or test hypotheses about the balance of nature, scientists simply assumed it must exist. Balance was a belief central to western faith in the human place in a divinely created world, for a lack of balance seemed to suggest a lack of divine order. If God were all-powerful, as most Europeans believed, then how could He allow the patterns of nature to be random and unpredictable? How could He allow a species He had created to go extinct? A belief in divine order led to a belief in natural order.

The seventeenth-century rationalists of the Scientific Revolution believed, even more strongly than had the Ancient Greeks, that laws governed nature, and that those laws were accessible to human reason. In thinking about the balance between predators and prey, they returned to the Ancient Greeks and, in criticizing their ideas, developed hypotheses of their own. For example, the English scientist Thomas Browne (1646) decided that Herodotus was wrong: lion cubs surely would never rip out their mothers' wombs. Instead, what kept predators and vermin in check must be hibernation: God must order all the noxious animals out of sight for the winter to give humans a break from their mischief. In 1662, John Gaunt came up with a new take on the regulation of predator numbers: wolves, lions and foxes were excessively fond of sex, and so much promiscuity limited their fertility.

These arguments may seem absurd now, but they reveal an important point about how strongly scientific ideas were shaped by cultural beliefs. People saw stability because they expected to see stability. Most people were aware of agricultural pests that wiped out entire crops, plagues of animals, and possible extinction of species. While these facts would have been difficult to reconcile with ideas of the balance of nature, the assumptions of balance were so fundamental to society that for centuries no one appeared troubled by the contradictions. Plagues, pests and famine might seem to indicate a world out of balance, but surely that was only in human terms: God had made the world go out of balance for his own divine purposes, perhaps to punish sinners.

What creates balance? Relationship between species

Most popular ecological thought now assumes that what keeps nature balanced is not divine order, but instead relationships between species: the "web of life." Deer numbers won't explode in a pristine system, people assume, because wolves keep their populations in check, leaving just the right number of deer that the habitat could support. Although few modern ecologists would agree with the details, relationships between species is still a topic that absorbs many many ecologists (see Chapter Eight). Before the eighteenth century, however, biologists had shown relatively little interest in the ways different species interacted. In the eighteenth century, with the Swedish scientist Carl Linnaeus (1707–1778), the focus changed from species in isolation to interactions between species, and the role that might play in keeping populations in check and nature predictable and balanced.

Before Linnaeus, most plant biologists had focused on individual species, rather than on plant communities and the complex interrelationships between plants and animals. Scientists asked few questions about why things lived in the places they did, why one tree was here, another there. Trees were there because that was the place God put them; not because of biological relationships—not because one plant altered its habitat, making it possible for another plant to survive. Most scientists thought of nature as unchanging, at least on any time scale that might matter to humans. Seeing the land as a static entity, rather than a place whose history was shaped by complex biological relationships, allowed people to simply pull out certain pieces—beaver, for example—without worrying too much about the indirect effects on the rest of the community. If the Earth was a collection of separate entities, then people had two alternatives: they could either admire those pieces, or extract them and use them. But few scientists expressed the thought that people were there to participate in an ecological community held together by a web of biotic relationships (Langston 1995).

Linnaeus, like his predecessors who focused on individual species, believed that each species fit into a precise place in nature's order, and that classification could help people perceive the underlying pattern in God's design. Linnaeus was determined to reduce the overwhelming complexity of natural history to a semblance of order, and this motivated his enormously influential system of classification for plant and animal kingdoms. Unlike his predecessors, Linnaeus believed it critical to understand relations between species, relations he believed had been designed by the Creator specifically to create order and stability—what he called the **economy of nature** (Egerton 1973). Centuries later, modern ecology dropped the assumption of divine design, but held onto Linnaeus' hypothesis that complex relationships between species created stability.

Linnaeus did not ask how such relationships developed, because like most of his fellow scientists, he assumed that God must have created them through divine wisdom. When, like many before him, Linnaeus asked what kept some populations of animals in check, the hypothesis that competition for resources in short supply might limit populations occurred to him. But he never examined this hypothesis closely, because the very idea of competition seemed to violate divine wisdom and harmony (Egerton 1973).

Linnaeus' interest in relationships between species was shared by the influential British naturalist Gilbert White (1720–1793)—one of the first natural historians to turn his passion for studying nature into an effort to preserve a natural order that seemed threatened by human industry. His 1789 work *The Natural History of Selborne* set out to understand the ways in which plants and animals interact with each other and their environment, creating a complex web of relationships and ordered beauty (Worster 1994). White, like Linnaeus, believed in a balance of nature endowed by God in which predators did not wantonly exterminate prey, but instead killed just the right amount to maintain numbers. Unlike Linnaeus, White realized that people could wreck that order. White realized that the nature he knew was drastically modified—and, he felt, badly damaged—by thousands of years of human activity. White longed for a time in the rural past when people lived in harmony with that nature, instead of destroying the balance of nature. His work was in many ways a precursor to modern environmental and ecological concerns, for White was among the first European biological thinkers to express a sense of the vulnerability of nature.

Succession and the balance of nature

One of critical developments in nineteenth-century science, during the period ecology was developing as a distinct science, was the awareness that nature has a history that shapes its present structure (Bowler 1993, Worster 1994). To us, it may seem obvious that the world changes through time, but for centuries few people believed this. The emergence of an historical view of nature was the source of enormous controversy, for it challenged the traditional view of a divinely created universe. Worster (1994) has argued that a growing sense of the Earth's vulnerability emerged from the realization that extinctions had happened in earth's history. A sense of history allowed people to see that extinction was indeed possible, forcing them to confront the possibility that humans might change the world in ways that could also destroy themselves.

As nineteenth-century scientists began to understand that extinctions had happened in the history of the Earth, other plant biologists began to focus on the roles of change and history on smaller time scales; i.e., within the development of an individual forest or meadow. Biologists began to focus not just on plants in isolation, as plant ecologists had for centuries, but also on the relationships between plant species, and on the ways those relationships affected the history of each in a given place. Noting which species tended to grow near each other, they asked how one kind of plant might affect the presence, absence, or growth of another plant.

In other words, biologists thought about the ways plants fit into communities. They saw the forest not just as a collection of individual trees, but also as changing patterns of trees in groups. This difference was critical. Once people started thinking about plant associations, they soon realized that they needed to consider the ways in which these plant associations formed—the history of communities as they grouped and regrouped. When people moved from seeing the forest as a collection of separate objects to a complex community, they were much more likely to imagine roles for change and history, as well as interconnections and indirect ecological effects.

This growing focus on the history of plant communities led to a critical concept in ecology: the theory of **succession,** which hypothesizes an orderly sequence of changes in plant communities leading to a stable climax community (Clements 1916, Christensen 1989, Finegan 1984, Perry 1995, Shugart 1984, Tobey 1981, Worster 1994). According to succession theory, changes in plant communities should follow orderly laws, and competition for space, light, and water would determine the patterns of those changes. After a disturbance such as fire destroys a forest, succession theory predicts that grasses would first invade the site, followed by shrubs that would crowd out the grasses. Soon certain tree species would displace the shrubs, and under the shade of the first trees, other tree species more tolerant of shade would come in and eventually eliminate the original species (see Chapter Three). Competition—for light, for water, for space—would determine the patterns of forest changes (Langston 1995).

Henry Cowles, working on the sand dunes of Lake Michigan (1899), formalized the idea of dynamic vegetational succession. After a major disturbance, such as a fire that burns down all the trees on a site, the first species to colonize are those that best exploit the conditions of the disturbed site—lots of sun but little water or nutrients. Soon, however, these **pioneer species** change the environment in ways that make their own continued survival difficult—they create so much shade that their seedlings cannot survive. They moreover cool the soil surface, contribute organic matter to the soil, and increase soil moisture, all of which favor the invasion of the community by more shade-tolerant species.

The idea of plant succession was not new; in his 60 A. D. *Natural History,* Pliny the Elder had described something quite similar. In the nineteenth century, Henry Thoreau, in *Natural History of Massachusetts* and *Succession of Forest Trees,* argued that shade tolerance was critical in determining successional changes. He suggested that oaks succeeded pines because young oaks could grow in the shade of pines, whereas pines could not grow in the understory unless the forest was thinned by burning or logging. With the development of succession theory, foresters gradually came to believe that what existed in a particular place was not only a matter of predetermined, abiotic factors, but also a product of biological history. A given plant existed in a particular place because of the other plants that had once been there.

Would succession continue forever, or was there some end to all that change? Frederic Clements (1916), one of the most influential ecologists of the twentieth century, proposed that succession led to a climax community—a stable community in which the vegetation was in equilibrium with the climate. When new species no longer changed the patterns of light intensity and soil moisture, succession stopped. Plants in the climax community could grow as well under their own parents' shade as those parents had grown under the species they replaced. Eventually all communities would arrive at the climax community determined by their regional macroclimate, and this community would have the potential to remain essentially unchanged forever. Different plant communities might begin with different species, but in a given climactic region they would all end at the same climax; i.e., climate and not biotic interactions determined the final community. Individual characteristics of the species on the site, local environment, soil, interconnections between plants and animals, disturbances such as fire and grazing, the plant and animal species available to colonize an area after disturbance, and finally chance—all these mattered little compared to the effects of climate. As Clements argued, the chance accidents of history mattered for only a short time, until finally the end point of succession was reached.

In Clements' theoretical framework, disturbance was a rare, external event, not an intrinsic property of the community. Succession, Clements insisted, was an orderly process. If ecologists could not predict the exact community that would come in after disturbance, they just did not know enough yet about the situation. Clements' ecological framework suggested an inevitability about the development of a community. It became an often-rigid orthodoxy that treated disturbances such as wind, fire, insects, and diseases as external influences that applied ecologists such as foresters could, and should, eliminate.

Clements' focus on holistic, interdependent communities grew partly out of his interest in the social philosopher Herbert Spencer, who argued that human society was similar to a biological organism. Each specialized trade in society was like an organ in the body such as the liver, providing functions that helped the whole but were also dependent on it. A liver could not exist for long outside the whole body, nor could the body exist without its liver. Likewise, the whole human community was more than the sum of its parts. Clements argued that natural communities could also be envisioned in these terms.

Clements was not the first to propose the concept of a biological community. Serious attempts to understand communities began early in marine biology and limnology. In 1877, Karl Mobius had originally suggested the biotic community concept in his study of oyster beds. Victor Hensen examined how plankton in the ocean functions, applying physiological methods to understand the annual cycles of plankton blooms in the ocean. His findings led him to argue for the importance of communities in marine systems. The limnologist Stephen Forbes, in his address on "The Lake as a Microcosm" (1887) explicitly emphasized that all species within a lake were linked into a functioning community that balanced predators and prey and formed something like an organism.

In America, the biologist Victor Shelford began to apply Clementsian concepts of community and succession to animals (Shelford 1913). He became interested in predator-prey relationships, food chains, and population fluctuations, asking many of the same questions about the regulation of animal numbers that had fascinated the Ancient Greeks. In Britain, the animal ecologist Charles Elton was also intrigued by these questions. Using the historical records of Hudson's Bay Company, Elton traced the fluctuations of fur-bearing animal populations (see Figure 1.1J). The cyclic relationship between lynx and hares seemed to suggest that predators controlled prey populations. However, Elton's continued research on fluctuations in animal populations eventually led him to repudiate the balance of nature concept:

> *The 'balance of nature' does not exist, and perhaps never had existed...Each variation in the numbers of one species causes direct and indirect repercussions on the numbers of the others, and since many of the latter are themselves independently varying in numbers, the resultant confusion is remarkable (Elton 1930).*

Wildlife ecology and the balance of nature: Predators and prey on the Kaibab Plateau

Generations of American students have learned about the balance of nature, the regulation of animal numbers, and the relationship between predators and prey from an ecological disaster reported to have taken place on the Kaibab plateau north of the

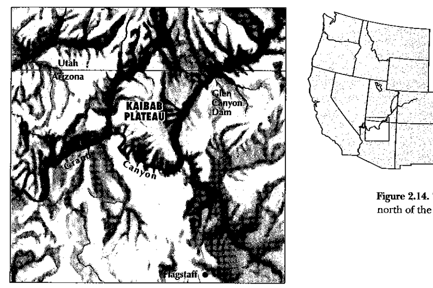


Figure 2.14. The Kaibab Plateau lies north of the Grand Canyon.

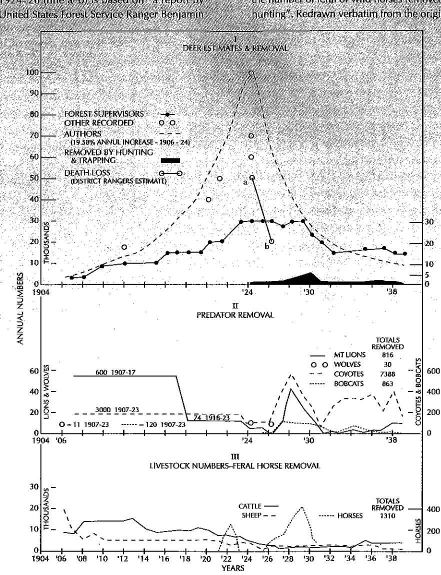
Grand Canyon (Figure 2.14; Young 1998). On this plateau, President Theodore Roosevelt established the Grand Canyon National Game Preserve in 1906, hoping to protect mule deer from destruction by hunting. Across North America in the late nineteenth century, unregulated commercial hunting had devastated wildlife populations, and many Americans were convinced that protection was necessary if wildlife was to remain part of the North American continent. Conservationists felt that deer needed to be protected from commercial hunters, sports hunters, Native Americans, and especially predators such as wolves.

Beginning in 1906, hunting was stopped and predators were killed across the plateau. In response, deer populations began to climb. Their populations increased from about 4,000 in 1906, to between 20,000 and 100,000 by 1924, according to various estimates (Young 1998). The native vegetation could not support such large herds, and deer began to die of starvation and disease. In 1924, the Secretary of Agriculture brought together a committee of experts to investigate the situation; members disagreed on policies that would reverse the decline, but all agreed that they needed to develop a plan for "scientific management" of the Kaibab deer population (Young 1998).

Wildlife biologists subsequently focused decades of intense research on these fluctuations in deer and predator numbers. In his 1932 dissertation, Victor Shelford's student D. Irwin Rasmussen graphed the history of population swings on the Kaibab, a figure that has been reprinted in generations of ecology and wildlife textbooks (Box 2.1). The graph showed that as predator numbers collapsed, deer numbers soared: a relationship that seemed to support the hypothesis that deer populations were regulated by predation. Although Rasmussen did not publish his work until 1941, in 1933 Aldo

Box 2.1. Portrait of population change

D. Irvin Rasmussen's original 1941 graphs for "Estimated numbers of deer and removals; predator removal; livestock numbers and feral horse removal, Kaibab Plateau, Arizona." Data for I were collected by "forest supervisors' estimates," "men visiting the Plateau," and organized winter counts. The deer death loss of 1924–26 (line a–b) is based on "a report by United States Forest Service Ranger Benjamin Swapp, who was in charge of the area where the deer died." The dashed line represents an estimated population trend from 4,000 deer in 1906 to near 100,000 in 1924, an accumulative annual increase of 19.58%. Graph II "gives record of predator removal"; III "shows number of livestock permitted on the area and the number of feral or wild horses removed by hunting". Redrawn verbatim from the original.



Leopold used Rasmussen's graph to argue for the importance of predators in *Game Management*—the first wildlife biology textbook. As Rasmussen and Leopold well knew, many factors other than predation—such as climate, food, and competition from domestic livestock—also affect the regulation of animal numbers. But in succeeding generations of biology and wildlife textbooks, the message of the Kaibab deer became increasingly simplified. From the Kaibab story, students were taught that natural processes of population regulation such as predation kept nature in balance, and when people removed those natural regulations, disaster resulted.

Eventually, the ecologist Graeme Caughley called a halt to the simplifications in the Kaibab story. In 1970, he published an article in *Ecology* that pointed out how textbooks had distorted Rasmussen's original graph. Caughley called attention to forces other than predators that might have affected the Kaibab deer herd. Moreover, he stressed that even in the absence of human interference, natural forces such as predation may often fail to keep population numbers within limits that the habitat can support. Nature does not necessarily provide perfect, orderly regulation of any population of organisms.

The Kaibab deer story has also been held up as an example of the ways wildlife managers have sometimes manipulated ecological data to persuade the public to accept changes in their management policies (see Dunlap 1988). According to Dunlap, in the early 1920s the experts had easily reached a consensus that the deer herd needed reducing, but political pressures made it impossible for administrators of the preserve to act on the experts' recommendation. The implication is that ecologists performed the basic research demonstrating the importance of predation, but the wildlife biologists then applied that research poorly, failing to control deer herds because of political disputes between different federal agencies over control of the wildlife resource. Yet, as Chris Young (1997) argues, this is too simple an interpretation of the relationship between wildlife biology, ecology, politics and culture. The delays in reducing the deer herd came about as much because of valid scientific uncertainty on the part of the experts, as from political pressures. No clear division between pure and applied science exists, and much valuable basic knowledge about predators and prey has come from the careful work of wildlife biologists who are trying to manage game. As Young notes,

> *...Controversy is as much a part of science as observation or evidence. Scientists do not develop theoretical principles about nature in one setting then apply them unproblematically in another. A process of negotiation (some would call it trial and error) takes place in attempting to make sense of the natural world* (Young pers. com.).

Recent challenges: Is nature in balance?

Soon after Clements published his works on succession, a few scientists challenged his theories of a stable climax. British ecologists were dubious from early on, believing that the contingencies of place and history had more effect on forests than implied by the climax theory of succession. In Britain, the landscape clearly bears the marks of human intervention and history, and vast, stable climax communities were more difficult to envision than in the American landscape. The British ecologist Henry Gleason argued in 1926 that superficially similar plant associations in truth differed substantially in species composition from place to place—thus pointing to an important role of the specific site. Given enough knowledge about the particular site, ecologists still thought they had enough information to know exactly where history would take a forest. A few years later, Arthur Tansley proposed the concept of the **ecosystem,** a complex system consisting of "...the whole complex of physical factors forming what we call the environment" (Tansley, 1935). Few ecologists, however, believed that the chance events of history were very important, until ecologist Robert Whittaker (1953) argued that there was no absolute climax vegetation for any area. In the 1950s, biologists who studied ecological history using pollen also began seriously challenging Clements' work, for they showed that the vegetation of North America has been in continual flux for at least the past 40,000 years (Christensen 1989). Although these ideas about ecosystems, changing climaxes, and the possible confusions of history were enormously important within academic ecology, they had little influence on how most applied ecologists thought about managing nature, as the Kaibab example shows.

After World War II, a perspective on community change developed which saw landscapes not as climax communities, but as patches recovering from disturbances (Pickett and White 1985). Ecologist A. S. Watt in 1947 presented to the British Ecological Society his "Pattern and Process in the Plant Community," a talk many have argued was one of the most influential in ecology. This work led to the **patch dynamics** perspective, which views a community not as a stable, fixed assemblage of species, but as a mosaic of patches differing in successional stages (Loucks and Wu 1996). Within intertidal communities, waves help create a mosaic of shifting patches (Levin and Paine 1971, 1974). Forest ecologists have similarly argued that disturbance processes within many forests create a dynamic system of patches of different ages and composition (Botkin et al. 1972, Shugart 1984). In grasslands, animal ecologists examined the ways bison graze, rodents burrow, fires burn, and plants and animals compete and cooperate; all of these processes shape a dynamic landscape (Loucks et al. 1985; Wu and Levin 1994).

To envision this new model of nature, imagine a landscape as a multi-colored patchwork quilt (the patch perspective), compared to a solid green wool blanket (the traditional view). One can also understand this change in representations of the natural world by considering a similar shift in representations of the political world. Figure 2.15 shows three maps of Africa, one from 1913, one from 1939, and one from 1983. The earlier map is dominated by lands ruled by the British and French empires (parallel to the climax community). But the second map looks different; the new mosaic reflects the ways political boundaries rapidly changed after the post-colonial revolutions and disturbances of the century. The third map shows yet another distribution of patches, as the boundaries shifted again after wars in the late twentieth century. These political maps offer one clue to the question: Why do the new ecological models of disturbance and flux seem more plausible to many people than the former equilibrial models? Since World War II, political and cultural changes have been rapid and often bewildering. Disturbance and uncertainty now seem more natural than harmony and equilibrium to many people, and this cultural climate may have helped the new ecological models seem more plausible than the former equilibrial models.

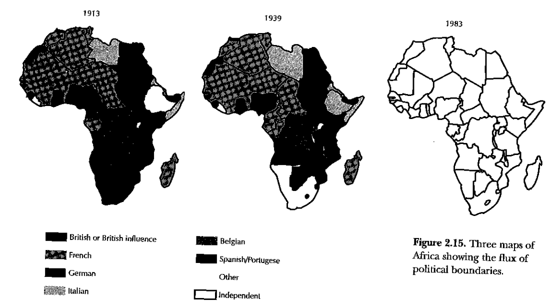


Figure 2.15. Three maps of Africa showing the flux of political boundaries.

How do ecosystems persist?

Ecologists still debate the question that puzzled the Ancient Greeks: how do ecological systems persist in the presence of forces that seem potentially destabilizing? As we've noted, ecologists now envision the landscape as a set of patches fluctuating in time and space, rather than a set of static climax communities. Few ecologists would argue that those dynamic patches are completely random collections of species, able to change into any other assemblage of species at any time. Many forests persist as forests in spite of thousands of years of disturbance, even though the patches within that forest may be changing. Other forested sites may, after a disturbance, be supplanted by scrub and grass. Most ecologists would now argue that neither of those forests was balanced or random, but instead that they had different levels of **resilience to disturbance**—defined as the ability to undergo change and then return to a similar, but not exact, system configuration (Perry 1995). Resilient forests, such as the New England forests discussed early in the chapter, may experience catastrophic events such as logging or enormous wildfires, but eventually trees return. But on a site that has been degraded past its ability to respond to disturbance, such as the Mediterranean forests, trees may not be able to recolonize and the forest disappears.

Resilience does not mean an absence of change; instead, it refers to what happens after the change. Ecosystems usually gain resilience not just because of the properties of individual organisms, but because of intricate ecological relationships (Perry 1988). These relationships are dynamic rather than stable, fluctuating over time as climates and ecosystems change. Actions that upset those relationships, however, may bring about unpredictable, undesirable, and irreversible changes. For example, even when fires repeatedly volatilized nitrogen from the soil, much of the American West still supported forests, perhaps because such nitrogen-fixing plants as alder and ceanothus came in after fires, returning nitrogen to the soil. Later, when foresters excluded alder and ceanothus from clearcuts because they had no commercial value, they introduced a new disturbance that reduced the system's ability to respond to other disturbances. If people alter a system beyond a threshold by breaking up ecological relationships, that system may lose resiliency and return to a new (and from a human perspective often much less desirable) community after a major disturbance (Perry 1988).

Disturbance and stability

Whether you see stability or chaos when you look at the world depends on your perspective. When you kneel on the ground and look very close, patches can seem random and chaotic, but when you stand miles away and see an entire **watershed**, those chaotic changes appear to even out, translating into a dynamic stability. In a forest, individual tree falls or forest fires can seem radically destabilizing and chaotic. But at the scale of watersheds, disturbances can create a shifting mosaic that may be stable. For centuries, roughly the same percentage of the watershed may contain stands of old-growth forest at any given time, even though the locations of those old growth stands will move as disturbances move through the forest, as trees age and die, and as new stands regenerate (Wu and Loucks 1996).

For thousands of years, people in western cultures have viewed disturbances—fires, windstorms, insects, disease—as destructive processes that destroy stability. But now many ecologists argue that from a long-term perspective, repeated disturbances may actually help maintain diversity and increase the chance that a given ecological system will persist. "Harmony is embedded in the patterns of fluctuation, and ecological **persistence** is 'order within disorder'" (Wu and Loucks, 1996). Patterns of disturbance can shape a diverse forest that over the long term may be much more stable than a forest protected from disturbance by people. For example, in western forests, fires of different intensities, along with storms, windthrows and insect attacks, together can create complex and shifting mosaics of forests across the landscape (Figure 2.16). Repeated light fires kept fuel loads (thick carpets of needles, branches, leaf litter, etc.) to a minimum, making huge, stand-replacing fires rare. When foresters tried to keep all fire out of the forest, the result was a community far more unstable in the long run, because it was far more vulnerable to intense fires that would remove the forest entirely from the site.

One of the critical insights of modern ecology is that human disturbances are now among the most important factors shaping ecosystem change. One hundred years ago, within mixed conifer communities in the American montane west, hot fires created gaps that let in pockets of sunlight where shade-intolerant trees such as ponderosa pine, larch, and lodgepole pine could establish in single-species stands. After a generation of human intervention in the form of fire suppression and logging, however, the effects of these intense fires have dramatically changed.

Think of a watershed as your hand, and the streams feeding into a watershed as the fingers on your hand (subwatersheds). Before logging and fire suppression, a catastrophic fire might have burned all the cover along one of those streams, but other streams with intact mature forests along them buffered the disturbance to the entire watershed. Twenty years later, cottonwoods and willows would have sprouted from the burned-out stumps, while ceanothus would have formed a thick low canopy that protected the soil from heavy rains. Across the stream, an old stand of ponderosa pine that had escaped the fire might have been ravaged by pine beetle. But a mile away, another patch of pine matured, another stand of spruce grew, and larch came in under a stand of lodgepole that had burst into flames. The trees shading another stream in

Figure 2.16. Fires, windthrow, and other disturbances shaped patchy forest such as these ponderosa pine stands in eastern Washington. From a photo courtesy of USDA Forest Service.

the watershed might have been blown over by a windstorm, but three streams still retained their old forest, and one stream had a recovered vegetation cover. Complexity buffered the disturbances.

If extensive clear-cutting and road building had denuded four of the streams, what would happen if a catastrophic fire destroyed cover along the stream with the only mature forest in the watershed? There would be nothing left to buffer the fire's effects across the land, no place for the animals whose habitats were destroyed to go, no mature trees left to seed in the burned site, and no pine forests nearby that could mature into old growth for another two hundred years. Whatever functions the mature forest naturally performed in the watershed would thus be missing from the system for centuries. This argument can also be extended to entire regions, especially when considering the effects of habitat loss on wide-ranging vertebrates such as spotted owls or pine martens (Perry 1995).

When ecologists point to evidence for dynamism in ecosystems, they focus on the most obvious (and directly economic) parts of the system: the plants. But large changes in the plant community, as in disturbance and succession, may be accompanied by much smaller changes in less obvious parts of the ecosystem—nutrients, soil structure, integrity of food webs. These relatively constant parts of the system may serve as legacies that maintain constraints on changes in plant communities. As these examples show, our attempts to say whether nature is balanced or dynamic depend on our perspective and the scale of our analysis. Many ecologists tend to dichotomize, calling nature either balanced or imbalanced, either stable or unstable—but nature works in many more than two modes (Perry 1995).

How Do Ecological Theories Change the Earth?

The science of ecology has dramatically shaped our current perceptions of nature. One good example of this is the way the term "ecology" can mean both the science and the political movement of nature preservation. Although one is a science and one is something very different, the political movement has borrowed deeply from the science. While many current ecologists may disavow their profession's links to the political movement, other ecologists now firmly believe that their research does and should aim to protect and restore the Earth's diversity and ecological functions. The science of ecology began, however, as a field devoted not to preserving natural relationships, but to better controlling them, and this goal affected the kinds of questions that were asked.

Foresters and succession: The Blue Mountains

Early ecologists, particularly in the United States, were motivated by the desire to use ecological knowledge to better manage ecosystems. For much of the twentieth century, scientists tried to use ecology to maximize outputs from public forests, hoping to minimize conflicts between different users who all wanted access to forest resources. They believed that maximizing production first required the liquidation of slow-growing ancient forests, so that rapidly growing forests could be grown instead. This management policy backfired, leading to devastating insect epidemics and fires across the West. Understanding how these ecological problems came about requires a look at the ways foresters have used ecological concepts of succession, competition, and climax communities, in their attempts to transform the forest (Langston 1995).

When Euro-Americans first came to the Blue Mountains of eastern Oregon and Washington in the early nineteenth century, they found a land of open forests full of large ponderosa pines—fire resistant, insect resistant forests that had been growing for centuries (Figure 2.17). But after less than ninety years of management by federal foresters, what had seemed like paradise was irrevocably lost. The great ponderosa pines vanished, and in their place were thickets of dying fir trees that were first attacked by defoliating insects (Figure 2.18), and then devastated by intense fires.

In part, the landscape changed for straightforward ecological reasons. When foresters suppressed fires in open, semi-arid, disturbance-prone forests dominated by ponderosa pine, firs grew faster than pines in the resultant shade—a successional change which left firs dominating the forests. Heavy grazing, which eliminated the grasses that had previously suppressed tree regeneration and kept forests relatively open, also contributed to the changes. High grading, or logging that removed old pine while leaving firs behind, also encouraged the replacement of open pine forests with dense fir stands. When droughts later hit, firs growing on dry sites succumbed to insect epidemics.

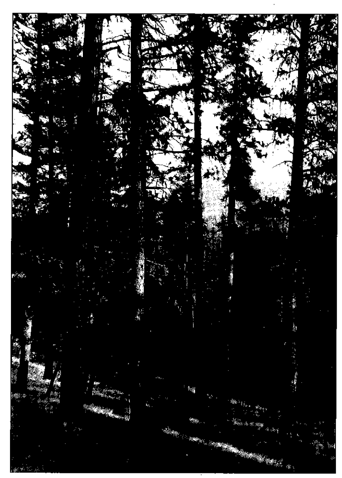


Figure 2.17. Open forests dominated by ponderosa pine were common in the Blue Mountains when Euro-Americans first arrived in the 19th Century. From a photo courtesy of National Archives, #95-G-320935.

But the real story is much more complex than this. Changes in the land are never just ecological

Figure 2.18. With the suppression of frequent, light fires, thickets of fir trees grew up in many forests. These dense stands were susceptible to attacks by defoliating insects, as shown in this illustration of the Yakima Reservation in eastern Washington, 1964. From a USDA Forest Service photo by R. G. Mitchell, Entomology Collection, PNW Research Station, La Grande laboratory, #PS-7990.

changes; people made the decisions that led to these ecological changes, and they made those decisions for a complex set of motives.

Federal foresters came to the Blue Mountains with the best of intentions: to save the forest from the scourges of industrial logging, fire, and decay. When they looked at the Blue Mountains, they saw two things: a "human" landscape in need of being saved because it had been ravaged by companies and the profit motive—and also a "natural" landscape that they felt needed saving because it was decadent, wasteful, and inefficient. Not only were federal foresters going to rescue the grand old western forests from the timber barons, they were going to make them better. Using the best possible science of the day, foresters felt they were going to make the best possible forests for the best of all possible societies—America in the brand-new twentieth century.

Industrial logging had been underway for less than a decade, and in that short time enormous changes were already beginning. Government foresters firmly believed that these industrial cutting practices produced sterile lands and, in particular, those practices destroyed the vegetation cover that protected the water supply in the arid west (Figure 2.19). Young trees were critical to the future of the forest, and industry seemed to have sacrificed them for short-term profits. Scientific forestry, the foresters felt, would change everything.

Two major interrelated tenets of scientific forestry developed. First, foresters felt they should encourage the growth of young trees by suppressing fire; and second, foresters felt they should replace old growth with regulated, rapidly growing forests. Fire seemed to threaten the forests by killing young trees, and since foresters were certain that young trees were the future of the forest, fire was clearly the enemy. The foresters thus decided that to protect the pine forests and the water supply, they needed to keep out fire and encourage reproduction. The Forest Service was convinced that the more young pines they had, the more merchantable pine would necessarily follow.

Although it was clear to early foresters that suppressing fire would lead to dense thickets of young trees, they felt that surely this would be a good thing, for reasons that show how their cultural beliefs affected their ecological reasoning. The early twentieth-century United States was a culture that glorified competition and masculinity. *Social Darwinism* promoted the belief that struggling with others for power and gain made men better men. Competition would eliminate the weak and favor the mighty. This ethos was fostered by emerging industrial capitalism and then projected onto the landscape. Foresters reasoned that dense stands of young trees would lead to intense competition for light and water, and that competition in the forest economy, just as in the industrial economy, would create vigorous individuals. Without competition, weaklings would

Figure 2.19. Early foresters believed that tree cover, as illustrated in this scene along a high-elevation stream in the forests of Eastern Oregon in 1929, protected the water supply in the semi-arid West. From a 1929 photo by N. J. Billings, U.S.D.A. Forest Service.

result—or so the foresters reasoned. The opposite turned out to be true, unfortunately. Western conifers do not self-suppress; without fires to thin them, what resulted was not a few big trees, but a thicket of stunted trees all the same age.

Replacing old growth with young trees was the second critical tenet of applied forest ecology. In 1905, the basic premise of the new Forest Service was simple: If the United States was running out of timber, the best way to meet future demands was to grow more timber. According to early Forest Service surveys, more than 70% of the Western forests were dominated by old growth. Foresters felt that meant western forests were losing as much wood to death and decay as they were gaining from growth.

Ecological theories of stability and predictability shaped the ways foresters viewed old-growth forests. Such forests, they thought, were at a stable, climax equilibrium, so the same amount of timber was lost to death and decay each year as was created through growth. Young forests would put on more wood volume per acre faster than old forests at equilibrium, since they were still growing rapidly. Therefore, foresters believed that young forests would create more wood for human use, so overmature forests needed to be cut down immediately. Scientific forestry seemed impossible until the old growth had been replaced with a regulated forest. These theories were not new; American foresters had borrowed them from European forestry, where old growth had long been eradicated. Trying to apply these European beliefs to a completely different set of ecological conditions in America shaped a Forest Service that, in order to protect the forest, believed it necessary to first cut it down.

When early foresters thought the forest would be improved if old growth were removed, their ideas about ecology were at the heart of their decision. These were ideas deeply shaped by their culture as well as by their science. Foresters seized on simple ecological theories—in particular, succession and competition theory—as a way of reducing the complexity of the forest to something they could hope to manage. Every species might be different, foresters reasoned, but with any luck they all followed the same simple rules. The alternative—that forest development might not follow orderly laws, and that nature might be so complex that people could never precisely predict the result of any action—was not something foresters wanted to contemplate.

Foresters interpreted succession theory in a particularly narrow way. Succession, they argued, was driven almost entirely by competition for light and moisture. In a struggle that approached warfare, each tree species tried to control limited resources. Forestry seemed to be simply a matter of manipulating nature's own competitive struggles, so as to tilt the balance towards economically useful species.

At the heart of forestry were two assumptions of competition theory: that the forest was a collection of resources, and that those resources were limited. There is only so much time in the world, so much energy, so much food. Tradeoffs are therefore inevitable: any time or energy spent on one activity is time taken from another activity. Any water you give out to the soil or to other plants is less water for you. Any nutrients another plant takes means less for you.

These assumptions stem from a vision of the world as a collection of separate, exchangeable parts. But there are other ways of seeing nature. One of the important insights of early ecological theory was that the natural world is not merely a collection of separate objects. Instead, indirect effects form an intricate series of relationships between the parts of a natural system. If a ponderosa pine releases water to surrounding shrubs, that does not always mean there is less for the pine. Those shrubs might in turn increase the local population of mycorrhizae, some of which might join with the pine and help it to better absorb nutrients from the soil.

Do the shrubs compete for resources with the tree? That question assumes a simple relationship of gain and loss; it is a human framework for seeing the forest, rather than the way the forest really is. Nor is the forest really an interconnected web of relationships—both competition and interconnection are human metaphors which help people work with the forest. But by focusing on competition theory and its applications to succession, early foresters discounted other ecological theories that were current at the time, particularly a recognition of the indirect effects that tied communities together. In their attempts to create an ideal, unchanging forest through competition, foresters had to discount these interconnected processes.

The assumptions of competition theory made it difficult for foresters to imagine that insects, waste, disease, and decadence might be *essential* for forest communities; indeed, that the economically productive part of the forest might depend on the economically unproductive part of the forest. But these semiarid, disturbance-prone forests were anything but efficient; their very inefficiency and redundancy was what allowed them to persist on dry, marginal sites. In trying to eliminate what they saw as wasteful insect enemies, foresters instead destroyed the habitat for the predators of those insects, making future outbreaks ever worse. In trying to eliminate what they saw as wasteful forest fires, they instead created conditions for ever more intense, catastrophic fires.

Scientific theories are important, but ideas alone do not shape the physical world. To transform the landscape, the right constellation of ideas, markets, ecological and economic conditions has to exist. At first, the Forest Service's dreams of transforming nature had little effect on the forest itself. Before the foresters could reshape the forests, they needed markets for the timber. And until the First World War, nobody was interested in buying federal timber. But after markets for Forest Service timber opened up, sales in the pinelands gained a momentum that quickly overwhelmed the conservative ideals of the foresters. All the sales were driven, not by the Forest Service's desire to make money, but by their firm conviction that scientific forestry would never be possible until old growth was eliminated.

To convert old growth to scientifically regulated forests, the Forest Service needed markets for that timber, and they needed railroads to get the timber out to the markets. Railroads were extraordinarily expensive, however. Financing them required capital, which meant attracting Midwestern lumber companies. But Midwestern corporations were only interested in spending money on railroads if they were promised sales rapid enough to finance those railroads. In the Blue Mountains, as across the West, this management policy devastated both the land and the local communities that depended on that land. Across the region foresters set up intensive harvests in the 1920s which would ultimately ensure that, by the late 1980s, harvests would drop by at least 60%, and mills would have little or no ponderosa pine left to harvest. This is exactly what happened—harvests collapsed and mills closed throughout the region. Ecologically, the effects were equally dramatic. Heavy logging, combined with fire suppression, high-grading, and grazing, led to the replacement of millions of acres of pine with thickets of drought-stressed, fire-susceptible firs.

The decisions of early scientists, while shaped by an ideology of efficiency and productive use, were not driven by individual greed or stupidity. Foresters destroyed the forests not in spite of their best intentions, but because of them—precisely because foresters' ideas of what was good for the forest were based on an ideal of deliberately transforming nature to serve industrial capitalism.

Early foresters had hoped that science would let them properly manage public forests for the public good, rather than for private gain. Only scientific experts, they felt, could solve public land conflicts. But what they did not realize was that their science was far from unbiased. It was deeply shaped by their culture, and this shaped a series of decisions that led foresters to attempt the transformation of old growth into productive, profitable forests. Anytime people use science in the formation of resource policy, they must grapple with these dilemmas. Scientific understanding is always simpler than the ecosystems; no one can ever understand everything about the ecosystems they are hoping to manage. Yet management is necessary, and ecology is one of the best tools for doing so, even if ecology can never offer a complete understanding of the entire world.

Does flux in nature justify transforming nature?

Fire suppression in the Blue Mountains illustrates a situation where beliefs in predictable succession, equilibrium, and climax communities helped justify intensive efforts to manipulate nature in order to increase production for human commodities. A belief in the balance of nature convinced many people that humans could never really upset that balance. Given enough time, people believed that succession would heal the wounds of human activity; people could therefore manipulate ecosystems without worry, since natural compensating mechanisms would eventually restore harmony (Bowler 1993, Christensen 1989).

Equilibrium models assumed that disturbances such as fire were external to the ecosystem. Many managers took this assumption one step further, attempting to remove these "external" disturbances to create a system they thought would be more balanced and stable. The Blue Mountains example is only one where this attempt to remove fire and increase stability badly backfired. Similar attempts at fire suppression around the globe have had equally dramatic and unintended

effects (Pyne 1982, Goudie 1994). In Alaska, fire suppression in lowland sites has led to an increase in moss, which densely carpets the ground, raising the permafrost level, in turn encouraging the growth of black spruce—an unpopular species among foresters, for it has little timber or wildlife value. Ironically, fire suppression ultimately can magnify the effects of fire, as the geographer Carl Sauer (1969) pointed out nearly three decades ago:

> *The great fires we have come to fear are effects of our civilization. These are the crown fires of great depths and heat, notorious aftermaths of the pyres of slash left by lumbering. We also increase fire hazard by the very giving of fire protection which permits the indefinite accumulation of inflammable litter. Under the natural and primitive order, such holocausts, that leave a barren waste, even to the destruction of the organic soil, were not common.*

Trying to remove disturbances can ultimately change an entire community, by changing the ecological relationships within that community (Goudie 1994). In South Africa, when Kruger National Park was established, white park administrators removed native peoples, for human hunters did not fit with the image of a pristine wilderness park. The native Africans who had lived in the area had set frequent fires to improve hunting. With the removal of the Africans and their fires, bush encroached onto grassland, reducing grazing for wild animals. Removing people to create an undisturbed, stable wilderness ironically harmed what the Europeans were trying to protect (Goudie 1994).

While models of nature's balance and stability justified some attempts to control nature by removing disturbances, many equilibrium ecologists such as the Odums were quite explicit about how they wanted their work used—to preserve rather than control nature. In contrast, current non-equilibrial ecologists have sometimes been far less interested in conservation or preservation. Donald Worster (1993, 1994) argued that part of the cultural appeal of disequilibrium as the norm of the natural world comes from people who want to blunt some of the more radical implications of environmentalism. As Worster argues, some of the ecologists who developed the initial theories about instability in nature were also fairly hostile toward environmentalism, justifying their hostility with a nod toward natural instability, and implying that since nature does not have a holistic balance, any human interference is acceptable—indeed even scientifically validated. For example, companies that specialize in genetic manipulations have argued that the new paradigm of nature's flux means that they can ignore the ecological implications of introducing created species into the environment. An article in the April 26th, 1997 *Economist* states that, since nature is a dangerous and unruly place regardless of humankind, people do not need to worry about introducing genetically manipulated plants. The implication is that, if there is no stable climax community, then no ecological relationship needs our concern. The image of the natural world as a place of competition, flux, chaos and instability provides for some people a justification for unrestrained human intervention in nature.

Many foresters have seized upon arguments about flux in nature, seeing them as permission for continued intensive management and extraction. If incessant, unpredictable change is the way of nature, why then bother to preserve any natural systems? If forests always change, then why worry about a web of interrelationships and interconnected effects? Why even bother to preserve any ancient forests, some people wonder, if they are all what one anti-environmentalist calls "fakes"—artifacts of humans (Budiansky 1995). As forester Henry Alden of the Michigan-California Lumber Company said in a 1992 speech,

> *The impact of the fire was more intense than any clear-cut I have ever seen...If fire is a natural and essential part of the ecosystem we have been far too delicate in our attempts to simulate the natural cycles of the forest.*

Likewise, some people now justify their calls for logging old growth forests by saying that, since recent ecological theory shows there is no balance in nature and no stability in diversity, old growth has no special value and should be removed to make way for tree farms (Chase 1995, Budiansky 1995). Chase and Budiansky have argued that if people are part of nature, and all ecosystems change, then people can do whatever they like to the land, since any changes thus caused are not degradations but merely new directions for the ecosystem.

Much of the appeal of earlier equilibrial models of nature's balance came from cultural beliefs; the same is surely true of current dynamic models of nature. But when anti-environmentalists argue that new ecology proves their claims, they are not basing their arguments in science, nor does this show that new ecology creates anti-environmentalism. People have always looked to scientific theories to support their political claims; that does not mean the scientists who came up with the theories share the same political beliefs.

Although some anti-environmentalists interpret dynamic ecology in ways that radically devalue non-industrialized ecosystems, a belief in the importance of disturbance history in ecosystems does not necessarily foster disrespect for nature. Much of conservation biology is based on the belief that humans can have profound effects on nature; therefore, people need to make changes only with great caution. Theories of dynamic, changing ecosystems can lead as easily to a respect for nature's extraordinary complexity, as to the opposite. If people are connected to the land in intricate but poorly understood ways, there can be no stronger argument for living with ecological respect, as part of an interdependent community (Grumbine 1992). Respect for the complexity and interconnections of ecosystems need not imply a belief in static equilibrium conditions. Instead, such respect recognizes value not just in what the land can give, but in a larger set of communities and processes which include but are not controlled by humans.

The new field of **adaptive ecosystem management** attempts to use some of the findings of dynamic ecology to manage natural resources, not for maximum commodity production (a traditional industrial forest), or for preservation of current conditions (a traditional reserve), but for the perpetuation of patterns and processes that allow the ecosystem to persist. Adaptive ecosystem management rests on several critical principles. First, all ecosystems change, often in ways that are difficult to predict. Because humans have influenced ecological processes and patterns for thousands of years, understanding human disturbances is important for understanding current ecosystem functions. Management must therefore pay attention to the changing human framework as well as to a changing natural framework. Traditional management tried to manage forests by removing elements that seemed unproductive. Adaptive management recognizes that all species and processes may play important roles in the forest ecosystem—even if these functions are not yet understood. Therefore, instead of trying to make natural ecosystems more efficient by removing whatever is not a useful human resource, adaptive management tries to maintain, restore, and mimic natural processes.

Adaptive management is not a new idea; it is simply a way of applying the scientific method to management. Nearly a century ago, Frederick Ames (1910), who first worked for the Forest Service in the Blue Mountains and then became Chief of Silviculture for the nation, warned his fellow foresters that they had to practice something akin to adaptive management. Ames argued that before foresters could begin to manage the western forests, they needed to recognize that they did not understand the forests well enough to predict their response to management. Nevertheless, they had to manage, and even doing nothing at all was a form of management. Therefore, what they had to do was treat "all of sales as a vast experiment." Ames outlined an extremely ambitious monitoring plan: after each timber sale, foresters would go in every three years and record the response of the site to whatever experimental treatment—also known as logging—they had devised. Over the next 100 years, they could then compare the effects of different kinds of logging, fire exclusion, and grazing on different forest conditions. Ames called for close attention to both the forest and the effects of human actions on the forest. In modern terms, Ames was telling his foresters they needed to practice "adaptive management" that recognized foresters could not always predict the effects of their actions.

This was an excellent idea, but unfortunately it did not work at the time, for practical and political reasons. Even when conscientious foresters gathered all the data Ames called for, these reports accumulated dust, first on the top of the supervisor's desk, then in the office's filing cabinets, then in cardboard boxes in the storage attics. No one knew what to do with all this information, and it continued to multiply exponentially while managers tried to figure out a solution. When foresters did try to monitor the effects of their logging practices, superiors in the regional offices usually shied away from making recommended changes, often for political reasons. Caution seemed easier than adapting to uncertainties, given the pressures on foresters to make timber available for sale (Ames 1915, Langston 1995).

At best, adaptive management is a way of monitoring the results of tree cutting, burning, favoring pine or anything else. But what is most innovative and promising about adaptive management is the way it tries to meet head-on the challenges outlined in this chapter: how do you manage in a world where you know that your models of the forest are always much simpler than the forest itself? In the words of Jack Ward Thomas, the wildlife biologist who attempted to bring adaptive management back to the Forest Service in the 1990s:

> *The forest is an extremely complex place; in fact, it is too complex for us to ever hope to understand.*

Nevertheless, one still has to manage it; no neutral position is possible—doing nothing is also a management strategy. All attempts to manage are attempts to tell a story about how the land ought to be, and by definition, all these stories are simpler than the world itself.

As the first foresters in the Blue Mountains recognized, everything resource managers do is nothing more, and nothing less, than an experiment. The critical step for management, however, comes after the experiment: using all that information to change how you work with the land. Here the young Forest Service found itself unable to resist pressures to continue business as usual. Monitoring does not necessarily mean big government programs; what it means above all is people on the ground being responsive to what the land is telling them, and being responsible for acting on that knowledge. It means a dialogue between people and land; it means people knowing the place they log, and knowing the place they work.

Science, like management, works best when it is adaptive. Early foresters came to the natural world with a set of general models borrowed from ideas about competition for light and water, and these rules allowed them to try to make sense of ecological patterns. More importantly, they enabled ecologists to see these patterns in the first place. These models were simplifications, but they gave foresters a way of seeing so they could notice something more than just a lot of trees. Some philosophers of science have argued that scientific models determine what you notice, and therefore blind you to what does not fit your models (Foucault 1980). Nonetheless the alternative is even more blinding. If you go out without a set of rules and questions, you do not see anything at all: the differences are lost to you. Your eyes are closed to the fact that spruce never grows in the open, that larch stands change to fir stands after a time, that lodgepole changes to spruce, that ponderosa pine stands change to fir. You see a static mass of green, not a history of change or a forest in motion.

The underlying lesson of these stories about the difficulties faced by earlier ecologists is not that they were wrong and unenlightened. The lesson is more complicated: all hypotheses are only partial models, simplifications of the world that are influenced by the cultural lenses with which we view nature. Yet those models engage the scientist with the world in an important way. The scientific method requires that the scientist approach the world with an open mind; as a scientist, you are supposed to treat your own ideas with humility, modifying your hypotheses if the results do not support them. This process is never completely open-minded; initial ideas about how the world ought to work shape how you construct hypotheses, what you see when you set out to test those hypotheses, and what you think worth noting down. But there is an important ideal here: you allow the natural world to shape your ideas, not the other way around. The history of ecology has consisted of a long series of negotiations with the natural world, which have allowed better management and restoration of ecological systems. Ultimately, all models are wrong—but they are still useful. When new data refutes or complicates current models, the result is an increased understanding of the world that makes the new models better approximations of nature. Ecology cannot offer a pure view of the world, untinged by politics and uncertainty. But it is still essential as a tool to make human relationships to nature more sustainable.

TECHNIQUES SPECIFIC TO ECOLOGICAL HISTORY

Reconstructing past landscapes and understanding the patterns of change in those landscapes requires the diverse tools of a detective. Ecological historians use documentary sources including old maps, photographs, corporate records, travelers' accounts, local histories, early scientific reports, farm account books, land survey records, letters, diaries, tax records, and old court cases. They also use field sources, such as pollen records, tree rings, and stumps in a forest, which provide information preserved in the landscape instead of in an archive (see Whitney 1994 for an excellent review).

For North America, written materials are available since European settlement. Many explorers and settlers recorded their impressions of the landscape in copious notes, diaries, memoirs, and reports. Although these are usually qualitative impressions rather than quantitative sources, they are nonetheless valuable. They do need to be used with caution when attempting to reconstruct the preindustrial landscape, for many of the sources reflect as much about the authors as they do about the landscape. Promotional tracts from land companies trying to attract buyers tended to exaggerate the fertility of the soil and the size of the trees, while settlers accustomed to forests tended to exaggerate the poverty of Midwestern prairie landscapes in their letters and journals (Whitney 1994). Legal documents are also useful; bounties on wolves, regulations of tree cutting, laws about fire use, drainage laws, game control, flood control regulations and water law all provide information about changes in the landscape.

In North America, early scientists provided extensive records from the turn of the century on ecological conditions. These records contain a great deal of quantitative material as well as qualitative impressions, so they are particularly valuable. Map series depict the changes in forest cover for many townships in North America. In the West, photographs of the changing landscape provide clues to succession, deforestation, urbanization, and effects of grazing. Aerial photographs, beginning from the Second

World War, provide larger scale views of a changing landscape. Census reports detail changes in agriculture and forest cover and soil productivity.

Land survey records are particularly valuable for North America, which is one of the few places on Earth that possesses detailed survey records describing vegetation before major transformations by European settlement. Survey records provide a qualitative and quantitative record of the pre-settlement forest, making it possible to derive tree species composition, size-class structure, and density of the forest communities. Yet these surveys need to be used with caution, because fraud and incompetence were not unknown among the early surveyors. Certain surveyors did their surveys from a bar stool; others misidentified trees, and some seem to have been biased in favor of the easiest routes across the territory they were surveying. Nevertheless, the land survey records are our best source of information on the preindustrial forests of North America.

While many sources offer clues to the American landscape that greeted European settlers, it is critical to remember that this is not the natural or original landscape. Rather, it is a historical snapshot of one moment from the past—a moment that occurred before extensive industrial transformations, but came after a long history of interaction with people. Learning how different native peoples lived on the Earth presents another set of challenges. Interviews with tribal elders provide useful information about the twentieth century; for earlier periods, ecologists, anthropologists, and archaeologists reconstruct past practices with pollen histories, fire histories, the records of early explorers, and interpretation of cultural stories. Archaeological studies of changing resource use can be particularly fertile sources (for example see Grayson 1993).

Landscapes contain a great deal of information about their own disturbance histories. Box 2.2 explains the ways that pollen records can help understand the past. Observation of current plant communities can also give clues to the past. Walking through many North Carolina piedmont forests, it is easy to stumble across the furrows in the soil left by plows. These forests grew up in abandoned farm fields, and the marks of the plow are still visible decades later. Daffodils growing in the forest usually indicate the site of an old farmhouse, where homesteaders planted flowers to cheer the view. When you come across an oak or a maple with a wide, spreading crown in the middle of a dense forest (Figure 2.20), you can be fairly certain that tree is a relic of a pasture or farmyard, since competition for light and space means that trees growing up in a forest tend to have narrow crowns. The effects of fire, windstorms, insect epidemics, logging, and farming can still be seen in forests, sometimes for centuries after the event occurred. Cores from trees tell a great deal about the forest's history, since each tree ring tells about the year it was formed. Narrow rings mean the tree grew only a little during those years, perhaps because of drought. Wide rings mean the tree was growing rapidly; fire scars indicate when ground fires swept through the forest (Figure 2.21). Plants, in other words, provide clues to the conditions in which they grew.

Figure 2.20. Trees with wide crowns in a dense forest indicate that this woodland was once an open field.

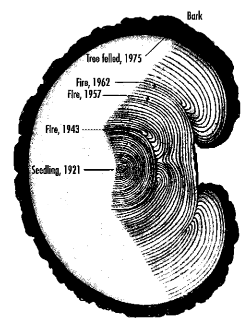


Figure 2.21. Tree rings offer clues to the history of the forest. Redrawn from Perry 1994.

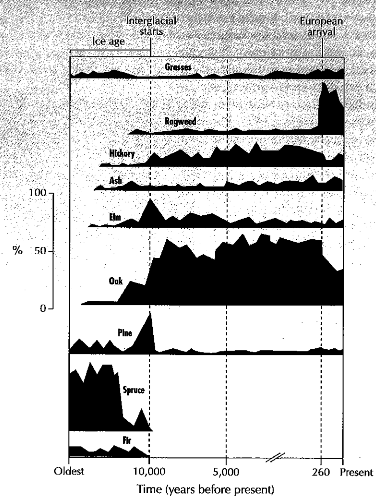
SUMMARY

Understanding ecological systems requires understanding the ways people have altered those systems, and the reasons for those alterations.

- Ecosystems are shaped by people as well as by ecological processes. Human events, as well as natural processes, help shape an ecosystem's history and its current patterns and processes.
- Ecology is a set of questions people ask about the complexity of life on Earth, not just a set of facts. The ways that scientists formulate hypotheses reflect their cultures as well as, the natural world that they are studying. Ecological ideas emerge in cultural contexts, and understanding the history of those ideas enables better understanding of the natural world.
- Scientific ideas affect how people transform ecological systems. Wildlife biologists, foresters, and other applied ecologists use ecological theories to manage nature. Modern debates about environmental degradation can only be resolved by understanding the complex cultural and scientific factors that have created those problems.

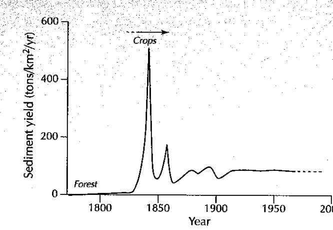
BOX 2.2. RECONSTRUCTING PAST LANDSCAPES WITH POLLEN RECORDS

Pollen history has proven to be a useful tool for reconstructing some past landscapes. In the spring, some trees, grasses, and herbs produce massive quantities of wind-blown pollen, as any allergy sufferer knows. Most of this pollen is decomposed by soil microbes or else destroyed by oxidation. Some, however, is captured in waterlogged lake sediments, peat deposits, and acidic soils in bogs. Each year, sediments at the bottom of lakes accumulate, and those sediments preserve the pollen deposited during the year that the sediment accumulated. Over thousands of years, these pollen samples fossilize; eventually the mud at the bottom of an old lake will contain the history of the region since the lake's formation, with the oldest material at the bottom and the youngest at the top. Researchers drill into the mud, extracting a vertical core of mud and fossilized pollen. Back in the lab, scientists called paleoecologists—ecologists of past eras—identify and count the pollen at different layers, documenting a history of vegetation change.



Thousands of pollen diagrams have been constructed from the United States; one from Silver Lake, Ohio, is shown on page 50 (redrawn from Ogden 1966). About 14,000 years ago, the lake formed after the retreat of the last glaciation and the pollen record started. Reading from the bottom of the diagram, at 14,000 years ago, the pollen from fir, pine, spruce and grass are common, indicating that a mixed coniferous woodlands existed in central Ohio at the end of the last ice age. The combination of these species suggests that the climate was cooler and drier than now. About 12,500 years ago, oak pollen begins to increase, suggesting a warming climate. Spruce and fir died out at the site, unable to compete in the altered climatic conditions. A cold period at 9800 years ago shows a brief peak in pine, and then it rapidly declines as the climate warms, and elm and hickory increase. At about 260 years before present we see a sharp decrease in forest species and an increase in ragweed, a now-common farmland weed. These changes correlate with the clearing of the forest for agriculture, tracking the invasion of European settlers and the tilling of the land.

Other material in lake sediments can also provide valuable clues to the past. Charcoal from ancient fires preserved within the mud can provide information about fire history and climate change. For example, researchers have traced increases in erosion (diagrammed below) and fires following European settlement and clearing of the land for agriculture.



RECOMMENDED READING

PETER BOWLER. *The Norton History of the Environmental Sciences.* Norton, New York. 1993.
A useful introduction to the history of ecology, geography, geology, and meteorology.

WILLIAM CRONON. *Changes in the Land: Indians, Colonists, and the Ecology of New England.* Hill and Wang, New York. 1983.
A fascinating and readable classic on the environmental history of New England.

ANDREW GOUDIE. *The Human Impact on the Natural Environment.* MIT Press, Cambridge, Massachusetts,. 1994.
An excellent overview of human transformations of the Earth.

EDWARD J. KORMONDY, ED. *Readings in Ecology.* Prentice Hall, Englewood Cliffs, New Jersey. 1965.
A collection of classic ecology papers that shaped the development of the science.

NANCY LANGSTON. *Forest Dreams, Forest Nightmares.* University of Washington Press, Seattle. 1995.
A study of the ways forests, ecologists, and human cultures have changed over the past century, leading to current environmental crises.

LESLIE A. REAL AND JAMES H. BROWN. *Foundations of Ecology.* Chicago University Press. Chicago, Illinois. 1991.
This is a collection of classic discussions on ecology.

DONALD WORSTER. *Nature's Economy: A History of Ecological Ideas.* 2nd Edition. Cambridge University Press, New York. 1994.
A very readable and provocative history of ecology and environmentalism.

Chapter 3

LANDSCAPE ECOLOGY

Living in a Mosaic

Monica G. Turner

- **What is Landscape Ecology?**
- **Questions Asked by Landscape Ecologists**
- **The Role of Models in Landscape Ecology**
- **Techniques Specific to Landscape Ecology**
- **Applications of Landscape Ecology**
- **Links to Other Kinds of Ecology**
- **Summary**

...a Market Economy: ...Redistribution?

...ellman

...ten years of transition to a market
...has reopened debates about the pace
...ss privatization. Despite differences,
...gly similar diagnosis of Russia's cur-
..."institutions"—a catch-all phrase to
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...inspectors, regulatory agencies, finan-
...—these are the institutions that are
...obsession with prices and property
...formers and their advisers in the early
...in a market without the institutional
...Achilles heel of the Russian transition.
...the initial thinking and underlying
...of market-supporting institutions to
...es to reform.
...ignore the importance of institutions
...? The extensive written record of their
...wise. Indeed, rapid liberalization and
...es designed to create a critical mass of
...fend the reforms once introduced but