CHAPTER ONE

BIODIVERSITY AND ITS VALUE

The earth never tires:
The earth is rude, silent, incomprehensible at first—Nature is
rude and incomprehensible at first;
Be not discouraged—keep on—there are divine things,
well enveloped;
I swear to you there are divine things more beautiful than words
can tell.

Walt Whitman (1856), *Leaves of Grass*

This book is an exercise in applied conservation biology. The fundamental question of conservation biology is a critical one: how can the variety of life be maintained in perpetuity? How can we help preserve "divine things more beautiful than words can tell"? No one has an answer to these questions. But scientists have learned a few things about how nature works and what kinds of human activities are compatible and incompatible with life on earth. In this chapter, we first define biodiversity and describe its major components, then discuss why diversity has become an issue in the United States. This leads into a discussion of the values of biodiversity and why management of biodiversity has become a regrettable necessity today.

What Is Biodiversity?

In little more than a decade, biodiversity progressed from a short-hand expression for species diversity into a powerful symbol for the full richness of life on earth. Biodiversity is now a major driving force behind efforts to reform land management and development practices worldwide and to establish a more harmonious relationship between people and nature.

Biodiversity. A symbol? An issue? A driving force? It would be easier if biodiversity could be measured by the quantity of bird species in a forest, wildflowers in a meadow, or beetles in a log. But simplicity is not one of the virtues of biodiversity. Ecosystems are more complex than we can imagine. Our most intricate machines—say, a space shuttle and all its ground-control computers—are simple toys compared to an old-growth forest, its myriad known and unknown species, and their intricate genetic codes and ecological interactions. Just identifying and counting species is difficult enough. The almost infinite complexity of nature defies our best efforts to classify, categorize, or even describe.

A common misconception is that biodiversity is equivalent to species diversity—the more species in an area, the greater its biodiversity. However, biodiversity is not just a numbers game. On a global scale, maintaining maximal species richness is a legitimate goal and requires keeping global extinction rates low enough that they are balanced or surpassed by speciation. When we consider species richness at any scale smaller than the biosphere, quality is more important than quantity. It is not so much the number of species that we are interested in, it is their identity. Fragmenting an old-growth forest with clearcuts, for example, would increase species richness at a local scale but would not contribute to species richness at a broader scale if sensitive species were lost from the landscape.

Diversification can all too easily become homogenization. The greatest cause of homogenization worldwide is the introduction of nonnative plants and animals, often called exotics. Exotics are species that have invaded new areas due to accidental or deliberate transport by humans. Although species naturally disperse and colonize new areas, so that floras and faunas change continually over long periods of time, human transport and habitat disturbance have greatly increased the rate and scale of invasions. Many regions have nearly as many exotic as native species today. Introductions of exotics may increase species richness locally or even regionally, but they contribute nothing positive to biodiversity. Rather, they pollute the integrity of regional floras and faunas and often alter fundamental ecological processes, such as fire frequency and intensity, and nutrient cycles. Thus, whole ecosystems are changed. Regions invaded by exotics lose their distinctive characters. Every place begins to look the same. The result is global impoverishment. For these reasons, we emphasize *native biodiversity*, not diversity per se.

The important task is not to define biodiversity, but rather to determine the components of biodiversity in a region, their distribution and interrelationships, what threatens them, how we measure and monitor them, and what can be done to conserve them. These topics are the subject of this book. But because working definitions are helpful to summarize what we are talking about, we propose the following modification of a definition developed by the Keystone Dialogue (Keystone Center 1991):

> Biodiversity is the variety of life and its processes. It includes the variety of living organisms, the genetic differences among them, the communities and ecosystems in which they occur, and the ecological and evolutionary processes that keep them functioning, yet ever changing and adapting.

This definition recognizes variety at several levels of biological organization. Four levels of organization commonly considered are genetic, population/species, community/ecosystem, and landscape or regional. Each of these levels can be further divided into compositional, structural, and functional components of a nested hierarchy (Noss 1990a). Composition includes the genetic constitution of populations, the identity and relative abundances of species in a natural community, and the kinds of habitats and communities distributed across the landscape. Structure includes the sequence of pools and riffles in a stream, down logs and snags in a forest, the dispersion and vertical layering of plants, and the horizontal patchiness of vegetation at many spatial scales. Function includes the climatic, geological, hydrological, ecological, and evolutionary processes that generate and maintain biodiversity in ever-changing patterns over time.

Why bother with this cumbersome classification? Because nature is infinitely complex. Unless we try to identify and classify the forms of this complexity, we are likely either to miss something or become hopelessly confused. If something falls through the cracks in our conservation programs, it may be lost forever. With each loss biodiversity is diminished. The earth becomes a less interesting place.

Conserving biodiversity, then, involves much more than saving species from extinction. As implied by our characterization of biodiversity, biotic impoverishment can take many forms and occur at several levels of biological organization. Hence, steps must be taken at multiple levels to counteract impoverishment. Below, we review some conservation issues, goals, and problems that can be addressed at each of four major levels of biological organization. We emphasize that a *comprehensive* conservation strategy must integrate concerns from all levels of the biological hierarchy.

Genetic Level

Genes, sequences of the DNA (deoxyribonucleic acid) molecule, are the functional units of heredity. Species differ from one another and individuals within species vary largely because they have unique combinations of genes. Gene frequencies and genotypes (individual organisms with a particular genetic make-up) within a population change over time as a consequence of both random and deterministic forces. Random changes include mutations that create new genes or sequences of genes, and loss of genes by chance in small populations (called sampling error or genetic drift). Deterministic changes include natural and artificial selection, where some genotypes are more successful reproducers than others. In the long run, genetic change leads to evolutionary change as individuals adapt to different situations and pass on their new traits to offspring. Genetic diversity is fundamental to the variety of life and is the raw material for evolution of new species. We will discuss evolution briefly in Chapter 2.

Conservation goals at the genetic level include maintaining genetic variation within and among populations of species, and assuring that processes such as genetic differentiation and gene flow continue at normal rates. Without genetic variation, populations are less adaptable and their extinction more probable, all else being equal. Small, isolated populations are more likely to diverge genetically, having fewer chances for genetic mixing with other populations. But at the same time small, isolated populations are more likely to suffer from inbreeding depression caused by mating between close relatives, which may result in reduced fertility and other problems (Frankel and Soulé 1981). Small, isolated populations also are subject to random loss of genes (genetic drift), which restricts their ability to adapt to a dynamic environment.

Conservationists talk much about saving the earth's genetic resources. But with the exception of some agricultural crops, commercial tree species, populations of rare vertebrates in zoos, and a handful of wild populations, we know very little about genetic diversity. Land managers seldom think about maintaining biodiversity at the genetic level. If our vision of conservation is long term, however, genetic variation must be better understood for all organisms.

Species Level

The species level of diversity is probably what most people think of when they hear the term *biodiversity*. Although in some ways species diversity is the best known aspect of biodiversity, we should bear in mind that the vast majority of species in the world are still unknown. Of an estimated 10 to 100 million species on Earth (Wilson 1992), we have named only about 1.8 million (Stork 1992). Known species are dominated by insects, half of them beetles (Fig. 1.1). But many invertebrates, bacteria, and other organisms remain to be discovered, even in the United States. Hundreds of invertebrate species can be found in one square meter of soil and litter in an old-growth temperate forest (Lattin 1990). Even more amazing, Norwegian microbiologists found between 4000 and 5000 species of bacteria in a single

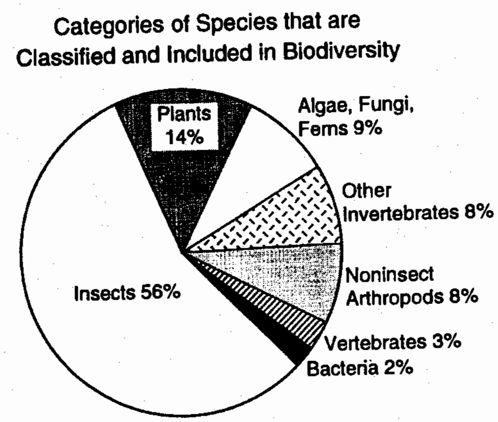

Figure 1.1 Taxonomic categories of species that have been named and described (adapted from Office of Technology Assessment 1987). Undescribed species, which outnumber described species by perhaps an order of magnitude, are probably mostly insects, other invertebrates, and bacteria.

gram of soil from a beech forest. About the same number of species, with little overlap, was found in a gram of sediment from off the coast of Norway (Wilson 1992). These findings raise the question of whether the tropical rainforests really are the most diverse habitats on Earth. We know too little about biodiversity to conclude much with certainty.

A population is a local occurrence of a species and is the unit that we usually manage. Conservation goals at the population/species level include maintaining viable populations of all native species in natural patterns of abundance and distribution. These goals grade into community-level goals of maintaining native species richness and composition, as discussed below.

Despite the problems and biases of single-species management, many species require individual attention, particularly when they have become so rare that heroic measures are needed to save them. In addition, certain kinds of species warrant management emphasis because their protection will conserve more than themselves. Especially important in this regard are keystone species, which play pivotal roles in their ecosystems and upon which a large part of the community depends (Noss 1991a). The importance of a keystone species is often disproportionate to its abundance. The beaver, for instance, creates habitats used by many species and also regulates hydrology and other ecosystem functions (Naiman *et al.* 1988). If we reduce beaver numbers through heavy trapping, then all else being equal, we impoverish the landscape. The beaver is not an endangered species, but it is greatly reduced or even absent from many regions where it was once abundant. Major declines of keystone species are more important ecologically than the loss of the last few individuals of rare species that play minor roles in their communities. This said, we must recognize that the term *keystone species* is poorly defined. Instead of a dichotomy of keystones and nonkeystones, communities may be better characterized by a wide range of interactions of variable strengths (Mills *et al.* 1993). Because we know so little about the ecological roles of species, each species must be considered important.

Some kinds of species have great pragmatic value for conservation, especially those we can characterize as "umbrellas" or "flagships" (Noss 1991a). To illustrate the umbrella concept, consider a carnivore (such as a grizzly bear or wolf) that requires millions of acres of land to maintain a viable population. If we secure enough wild habitat for these large predators, many other less-demanding species will be carried under the umbrella of protection. Umbrella species are often charismatic, so they also function as flagships or symbols for major conservation efforts. The grizzly bear, for instance, is a potent symbol for wilderness preservation in the northern Rocky Mountains. No umbrella is complete, however. Some endemic plant species have very small ranges—perhaps restricted to a single rock outcrop—that might not be protected in an ideal wilderness network established for grizzlies.

Animals and plants that are highly vulnerable to human activity often need to be managed individually, at least until their habitats can be protected by an ecosystem-level approach. Otherwise, biodiversity will continue to diminish with each extinction. Although we might accept the egalitarian notion that all species are ultimately equal, at any given place and time some species thrive on human activity and others suffer. Familiar examples of species that are extremely vulnerable to human activity are the northern spotted owl, threatened by logging of old-growth forests in the Pacific Northwest (Thomas *et al.* 1990); the red-cockaded woodpecker, endangered by logging of longleaf pine forests in the Southeastern Coastal Plain (Jackson 1986); and the desert tortoise, often shot or run over by motorized recreationists, forced to compete with livestock, collected for pets, and now ravaged by disease (U.S. Fish and Wildlife Service 1993). Species declines are signals that the environment is not healthy, but vulnerable species often require intensive care above and beyond immediate protection of their habitat.

Community or Ecosystem Level

In many cases, conservation is most efficient when focused directly on the community or ecosystem. A community is an interacting assemblage of species in an area. Terrestrial communities are usually defined by their dominant plants (for instance, the beech-maple forest), but functional or taxonomic groups of animals (for example, bird communities, lizard communities, herbivore communities) are also recognized. Functional groups of organisms (species that use a set of resources in similar ways, such as bark-gleaning birds) are often called *guilds.* Similarly, aquatic communities may be taxonomically or functionally defined, for example fish communities or littoral (shoreline) vegetation.

An ecosystem is a biotic community plus its abiotic environment. Ecosystems range in scale from microcosms, such as a vernal pool, to the entire biosphere. Many ecologists equate the terms *ecosystem* and *community,* except that ecosystem ecologists emphasize processes more than species and other entities. The Nature Conservancy defines natural communities by their most striking characteristics, whether biotic or abiotic. Thus, coastal plain pond, rich graminoid fen, black spruce-tamarack bog, and rich mesophytic forest are all described communities of New York State (Reschke 1990). These communities might also be called ecosystem "types." The variable spatial scale of ecosystems confuses the issue sometimes. Although scientists usually think of ecosystems as relatively discrete and existing at the same spatial scale as natural communities, conservationists often use the term *ecosystem* to encompass many different communities. For example, the Greater Yellowstone Ecosystem covers a diverse region of 14 to 19 million acres (see Chapter 5).

We consider conservation at the community or ecosystem level to complement, not replace, species-level management. The rationale for protecting ecosystems is compelling: if we can maintain intact, ecologically functional examples of each type of ecosystem in a region, then the species that live in these ecosystems will also persist. Representing all native ecosystems in a network of protected areas is the most basic conservation goal at the ecosystem level (see Chapter 4). Opportunities for adequate representation of ecosystems are being rapidly diminished as many of our native vegetation types are being reduced in area and degraded in quality (Noss *et al.* 1994).

Practicing conservation at the community or ecosystem level demands attention to ecological processes. Maintaining processes is not just a way to maintain species. Rather, processes are valuable for their own sake as part of the diversity of life. The processes that are most crucial for ecological health vary from ecosystem to ecosystem. In terrestrial communities some of the most important processes are fire and other natural disturbances, hydrological cycles, nutrient cycling, plant–herbivore interactions, predation, mycorrhizal interactions between tree and shrub roots and fungi, and soil building processes. All of these processes affect biodiversity at several levels and are included within our definition of biodiversity. They must be maintained within normal limits of variation if native biodiversity is to persist. Clearcutting and other intensive forest management may fail to conserve biodiversity because they disrupt nutrient retention and other ecological processes. Livestock grazing that interferes with basic ecological processes will also fail to conserve native biodiversity in rangelands.

Alpha, Beta, and Gamma Diversity

The variety of species in a defined area is one common measure of biodiversity at the ecosystem level. But to say that more diverse areas are better is misleading because measures of species richness or diversity neglect a most important consideration—the identity of species. One way to consider species diversity while paying close attention to species composition is to note the spatial scale of observation and how composition changes from one scale to another. The collection of species within an area of relatively homogeneous habitat is called *alpha* diversity or within-habitat diversity (Whittaker 1972, Karr 1976). Each site will have its own characteristic alpha diversity, although physically similar habitats in the same region can be expected to have similar species composition.

As we expand the scale of observation, we encounter variation in the underlying physical environment (environmental gradients). As we move along a gradient, say upslope, downslope, or from one soil type to another, we encounter new species adapted to these different conditions. The turnover in species along an environmental gradient is called *beta* diversity or between-habitat diversity. When we measure the diversity of species across several different habitats in a landscape, we are measuring beta diversity.

At a still broader scale, many environmental gradients are found and geographic replacements of species occur as range boundaries are crossed. Diversity at this regional scale is called *gamma* diversity. The alpha, beta, and gamma diversity concepts are useful for comparing biodiversity in different regions or in the same region under different management scenarios. Two regions of roughly equivalent gamma diversity may differ greatly in alpha and beta diversity. For example, Region A is mostly lowland forest with high alpha diversity but little habitat diversity. Thus, any site in the region is likely to contain roughly the same set of species. In contrast, Region B is mountainous, with tremendous differences in species composition between habitats but lower diversity within any single habitat. Generally speaking, a landscape in the eastern deciduous forest biome will have higher alpha diversity than many areas in the West. However, western landscapes characteristically have higher beta diversity due to the effects of aridity and topographic variation. Conservationists would have to consider very different scales and factors in planning reserve systems in the two regions. It is prudent to consider the maintenance of alpha and beta diversity within the broader context of gamma (and ultimately global) diversity.

Landscape and Regional Levels

If biodiversity occurs at multiple levels of organization, it is worth protecting at all levels. Forman and Godron (1986) defined a landscape as "a heterogeneous land area composed of a cluster of interacting ecosystems that is repeated in similar form throughout." Similarly, Urban *et al.* (1987) characterized a landscape as "a mosaic of heterogeneous land forms, vegetation types, and land uses." These definitions suggest that landscapes have a *pattern* and that this pattern consists of repeated habitat components that occur in various shapes, sizes, and spatial interrelationships. In many landscapes, this pattern consists of patches and corridors in a matrix, the matrix being the most common or interconnected habitat in the landscape (Forman and Godron 1986). Other landscapes are mosaics of many habitats, and the pattern is difficult to classify into discrete components.

We use the term *region* (also *bioregion* or *ecoregion*) to refer to large landscapes that can be distinguished from other regions on the basis of climate, physiography, soils, species composition patterns (biogeography), and other variables. Landscape or regional diversity is pattern diversity—the pattern of habitats and species assemblages across a land area of thousands to millions of acres—and can be considered a higher level expression of biodiversity. The pattern of species distributions and communities across a landscape has functional ramifications. Many animals, for example black bears, use more than one habitat type to meet their life history needs. We cannot protect these species by managing different communities in isolation. Bears and other wide-ranging animals are often important in dispersing seeds across a landscape. Disrupting bear movements by fragmenting the landscape may indirectly affect other species.

Adjacent habitats affect each other in many ways, including by microclimatic effects and transfer of nutrients, propagules, and disturbances across edges and ecotones. Because human activities often change landscape patterns, they have impacts on biodiversity that ripple through other levels of organization, affecting species composition and abundances, gene flow, and ecosystem processes. If a forest landscape is fragmented into small patches, those patches may experience a drier microclimate than the original forest, increased susceptibility to windthrow, loss of forest interior species, reduced genetic diversity within remaining populations, and invasion by weedy and exotic species (Burgess and Sharpe 1981, Harris 1984, Franklin and Forman 1987). These problems cannot be solved patch by patch, but only across all patches and their matrix. Hence, the regional landscape is an appropriate scale at which to identify important sites and patterns, and to manage and restore land for conservation purposes (Noss 1983, Turner 1989).

A primary conservation goal at the landscape or regional level is to maintain complete, unfragmented environmental gradients. This extends the representation goal beyond traditional ecosystem boundaries. Species richness and composition are known to vary along environmental gradients. The most commonly studied gradient is elevation. In the western Cascades of Oregon, the number of species of amphibians, reptiles, and mammals declines sharply with increasing elevation (Fig. 1.2). This presents a problem for conservation, because generally speaking, the low-elevation, high-diversity sites are private lands which are often heavily exploited and have few natural areas left. Mid-elevation sites are commodity-production public lands, and large protected areas (such as designated wilderness) occupy the high-elevation, lowest diversity sites. This biased pattern of habitat protection is common throughout the western United States (Davis 1988, Foreman and Wolke 1989, Noss 1990b). By contrast, in southeastern states with abundant wetlands, such as Florida, most wilderness areas are habitats too wet for commercial forestry. Preserving only the most species-rich sites or portions of environmental gradients is no solution, because different species occupy different portions. Alpine wildflowers are not found in the rich lowlands. Conservation programs must strive to maintain natural ecosystems and biodiversity across the full extent of environmental gradients.

The effects of natural disturbance on biodiversity often can be best appreciated at the landscape scale. Disturbances typically create patches in the landscape, of various sizes, that are used by different sets of species (Pickett and White 1985). Disturbance-recovery processes are complex. For example, most forest fires are mosaics of many different fire intensities, with some patches experiencing crown fires, other patches untouched, and a wide range of intensities in between. Recovery after fire varies with intensity (sometimes the soil may be sterilized and succession is slow), seed sources, weather, and other factors. Variability in disturbance regime is responsible for much of the habitat diversity found in natural landscapes. Generally speaking, the more diverse the habitat, the more species can coexist. However, diversification by disturbance has a limit. Actions that diversify habitat locally may reduce diversity at regional and global scales if disturbance-sensitive species are eliminated. Disturbance regimes will be discussed in more detail in Chapter 2.

In landscape ecology, context is just as important as content. Small reserves set aside for their content (for example, to represent plant community types or to protect a remnant population of a rare species) are heavily affected by their context when the surrounding landscape is altered. Eventually, a small reserve or a system of small, isolated reserves may fail to maintain the elements for which they were established. Natural fire regimes,

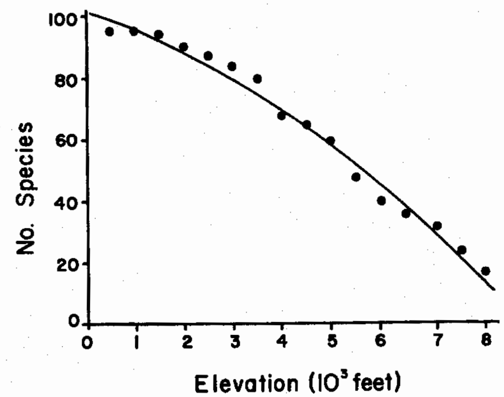

FIGURE 1.2 Relation between elevation and species richness of amphibians, reptiles, and mammals in western Oregon (from Harris 1984). The decline in species richness with increasing elevation is accompanied by a decline in density of individuals of all species combined. Used with permission of the author and University of Chicago Press.

migration of large animals, landform evolution, and hydrological cycles are ecological processes that can be perpetuated only by conservation at landscape and regional scales. Thus, a biodiversity conservation strategy is complete only when expanded to these scales.

Cultural or Social Diversity

Have we missed anything in our broad characterization of biodiversity? During the Keystone Dialogue on Biological Diversity and in similar forums, some participants insisted that human cultural or social diversity be included in the definition of biodiversity and in any strategy for its conservation. The Global Biodiversity Strategy (WRI, IUCN, UNEP 1992) makes this point strongly:

> Human *cultural diversity* could also be considered part of biodiversity. Like genetic or species diversity, some attributes of human cultures (say, nomadism or shifting cultivation) represent "solutions" to the problems of survival in particular environments. And, like other aspects of biodiversity, cultural diversity helps people adapt to changing conditions. Cultural diversity is manifested by diversity in language, religious beliefs, land-management practices, art, music, social structure, crop selection, diet, and any number of other attributes of human society.

On the face of it, inclusion of social diversity in a definition of biodiversity makes sense. We are fundamentally as much a part of Nature as any other species and share kinship and ecological interactions with all of life. But what would be the practical effect of including diversity of human languages, religious beliefs, behaviors, land management practices, etc., in a biodiversity definition and striving to promote this diversity in conservation strategy? We believe the effect would be to trivialize the concept and make it unworkable, even dangerous. As Kent Redford (personal communication) notes, "This definition allows Manhattan or Sao Paulo to be considered on equal footing with the Great Barrier Reef of Australia and makes impossible any coherent discussion of biodiversity conservation." We are not interested in maintaining social or cultural diversity if it means maintaining Nazis, slave owners, or those who enjoy using desert tortoises for target practice. This book is about how culture might adapt to nature. We want to conserve all cultural approaches that are compatible with conserving biodiversity. To combine cultural and biological diversity into one definition is to muddle the concept.

Why Has Biodiversity Become an Issue?

Why has biodiversity become an issue in the United States? Have conventional approaches to conservation failed? Consider the continent of North America 300 years ago. A description from an early explorer in Florida portrays the diversity of life in the Southeastern Coastal Plain, a richness paralleled in many different and glorious ways across the continent:

> We returned, viewing the Land on both sides of the River, and found as good tracts of land, dry, well wooded, pleasant and delightful as we have seen anywhere in the world, with great burthen of Grasse on it . . . the woods stor'd with abundance of Deer and Turkies every where . . . also Partridges great store, Cranes abundance, Conies . . . several Wolves howling in the woods, and saw where they had torn a Deer in pieces. Also in the River we saw great store of Ducks, Teile, Widgeon, and in the woods great flocks of Parrakeeto's . . . we measured many of the Oaks in several places, which we found to be in bignesse some two, some three, and others almost four fathoms; in height, before you come to boughs or limbs, forty, fifty, sixty foot, and some more. . . . Also a very tall large Tree of great bignesse, which some do call Cyprus. . . . (Hilton 1664, in Salley 1911)

The European explorers' impressions of a vast wilderness continent were accurate enough. All of this country was roadless, unpolluted, rich with wildlife, and incomparably beautiful. But this was not a wilderness "untrammeled by man," in the controversial language of our Wilderness Act of 1964 (Callicott 1991). The North American wilderness was a peopled wilderness, yet peopled sparsely and, for the most part, gently. An estimated 10 million native humans, 3 percent of the present human population, inhabited North America when the first white people arrived. In places the Indians modified their landscape considerably, especially through the use of fire (Day 1953, Pyne 1982). Hunting by their ancestors probably contributed to the extinction of large mammals near the close of the Pleistocene (Martin and Klein 1984). But native cultures occasionally enriched native biodiversity locally and perhaps regionally through diverse agricultural plantings (Nabhan 1982). Although the romantic notion of Indians as the original environmentalists is not entirely accurate (Callicott 1982), in general the native Americans seem to have lived in harmony with the rest of nature. Without such a relationship they would have had trouble persisting here for over 20,000 years. A culture that destroys its environment is suicidal.

The picture changed dramatically after the arrival of European settlers. The biological history of North America since then—a story seldom told in American history classes—has been one of profound impoverishment, particularly in the last 200 years. The slaughter of native Americans by early explorers and colonists is now well known, but the desire of Europeans for subjugation extended to other life forms as well. This subjugation continues today. In the words of Barry Lopez (1992):

> The assumption of an imperial right conferred by God, sanctioned by the state, and enforced by a militia; the assumption of unquestioned superiority over a resident people, based not on morality but on race and cultural comparison . . . the assumption that one is *due* wealth in North America, reverberates in the journals of people on the Oregon Trail, in the public speeches of nineteenth-century industrialists, and in twentieth-century politicians. You can hear it today in the rhetoric of timber barons . . . standing before the last of the old-growth forest, irritated that anyone is saying "*enough* . . . , it is enough."

European settlers saw the people, wildlife, and land of North America as something to be conquered, tamed, and subjected to their will. A concern for or even knowledge of what was being lost was altogether lacking.

As biologist Larry Harris describes it, "we swept across this continent so quickly . . . that we never really knew what was here" (quoted in Chadwick 1990). The great eastern deciduous forest exists today only as tattered remnants, growing slowly back in some regions, such as parts of the Northeast and southern Piedmont, but still being fragmented and subdivided in others. Cougar are gone from the East with the exception of a tiny population of Florida panthers on the verge of extinction in south Florida, and scattered but questionable reports farther north. The ivory-billed woodpecker, Carolina parakeet, Labrador duck, heath hen, great auk, and passenger pigeon (the most abundant landbird in the world when Europeans arrived) are gone from the earth, as are Merriam's elk, Audubon bighorn, the buffalo wolf, sea mink, and Caribbean monk seal. The estimated 40 million pronghorn that roamed the West before arrival of the pioneers were quickly reduced to fewer than 20,000. An estimated 60 million bison were reduced to fewer than a thousand by 1890 (Zeveloff 1988). The Boskowitz Hide Company of Chicago shipped more than 34,000 bison hides out of Montana and northern Wyoming in 1880. In 1884 they could get only 529 (Madson 1987).

These megafauna were only the most conspicuous losses. The Nature Conservancy estimates that over 200 full species of plants, plus many more varieties, and 71 species and subspecies of vertebrates have gone extinct in North America north of Mexico since European settlement (The Nature Conservancy 1992, Russell and Morse 1992). Over 750 species of plants and animals in the United States are federally listed as threatened or endangered, thus officially considered close to extinction. Another 3000-plus species are candidates for listing, yet at present rates of listing many of these candidates will be lost before receiving protection under the Endangered Species Act. Only five listed species have recovered enough to be removed from the list (Wilcove *et al.* 1993). The steady erosion of our native biodiversity is a direct consequence of the callous disregard we have shown for our environment and our evolutionary kin. This disregard continues today, ironically despite polls showing that 89 percent of the national public agrees with the statement "humans have an ethical obligation to protect plant and animal species" (Shindler *et al.* 1993).

Opponents of conservation often point out that extinction is natural and not worth worrying about. However, with the exception of a few mass extinction events in ancient geological history, the rate at which new species are created has exceeded the rate of extinction. Therefore, the number of species on Earth seems to have slowly but, with a few punctuations, steadily increased over time. That trend is being reversed today. As explained by Wilson (1985):

> No comfort should be drawn from the spurious belief that because extinction is a natural process, humans are merely another Darwinian agent. The rate of extinction is now about 400 times that recorded through recent geological time and is accelerating rapidly. Under the best of conditions, the reduction of diversity seems destined to approach that of the great natural catastrophes at the end of Paleozoic and Mesozoic Eras, in other words, the most extreme for 65 million years. And in at least one respect, this human-made hecatomb is worse than at any time in the geological past. In the earlier mass extinctions, possibly caused by large meteoritic strikes, most of the plant diversity survived; now, for the first time, it is being mostly destroyed. (Knoll 1984)

Recent extinctions and the ever-expanding list of endangered species in North America show that the biodiversity crisis is not just a tropical problem. Although current extinction rates in the tropics, estimated at somewhere between 10,000 and 150,000 species lost per year over the next few decades (Wilson 1988, Diamond 1990), are higher than in the temperate zone due to the apparently greater diversity of tropical systems, some North American ecosystems are more endangered than tropical rainforests and stand to lose as great a proportion of their species. Examples from the United States of natural communities being destroyed faster than tropical rainforests include freshwater habitats in California (Moyle and Williams 1990) and old-growth forests of the Pacific Northwest (Norse 1990). In 1992, newspapers throughout the country reported a NASA study showing that the loss of old-growth forests in the Pacific Northwest surpassed in rate and extent the clearing of the Amazon basin. Satellite photographs vividly compared the damage (Fig. 1.3). Earlier, a *National Geographic* article portrayed the loss of virgin forests in the 48 conterminous states (Findley 1990), which amounts to at least 95 percent of the forests that greeted the first European settlers. Ancient forests have finally captured the public's attention, but they are not the only ecosystems disappearing. Estimates of ecosystem decline throughout the United States are shockingly high (Noss *et al.* 1994). We have already lost far more than most Americans realize.

Why Are We Concerned About Biodiversity?

Aldo Leopold (1953) observed: "The last word in ignorance is the man who says of an animal or plant: 'What good is it?' If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If

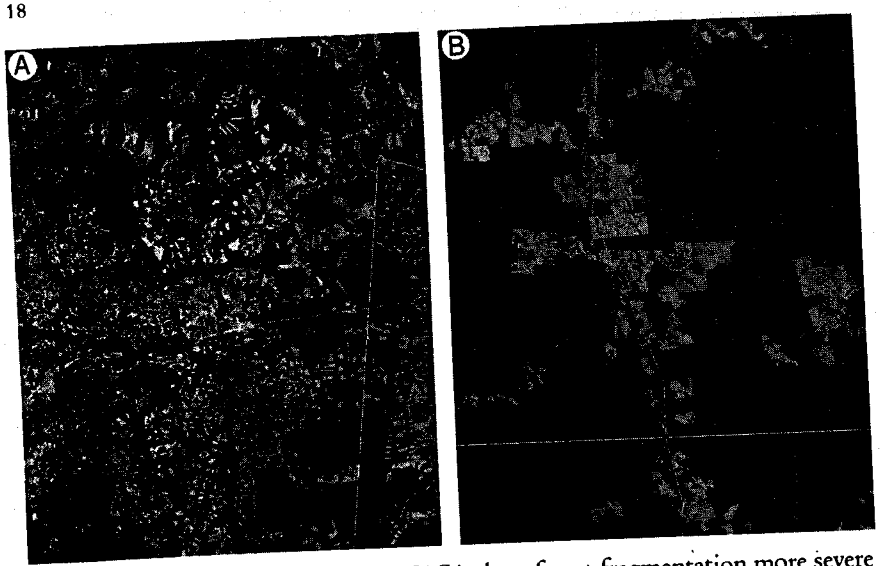

FIGURE 1.3 Satellite images from NASA show forest fragmentation more severe in the Mt. Hood National Forest of Oregon (A) than in the Amazon basin of Brazil (B). Source: NASA/GSFC (1992).

the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering."

Do people care if species go extinct and natural areas are converted to shopping malls? Public opinion polls in the United States show that Americans are concerned about endangered species. For example, a recent poll of 1000 registered voters spanning the demographic, political, and geographic spectrums of the U.S. showed that 66 percent support the Endangered Species Act and only 11 percent opposed protecting endangered species (Stolzenburg 1992). Another poll showed that 78 percent of the national public believes that greater protection should be given to fish and wildlife habitats on federal forest lands; 65 percent disagreed with the statement that endangered species laws should be set aside to preserve timber jobs (Shindler *et al.* 1993). Although these polls asked mostly about species, not ecosystems, we can expect that many people will oppose destruction of natural areas, especially areas near and dear to them.

Are there more fundamental reasons for protecting species and ecosystems, besides public support for such actions? Many texts have examined the values of biodiversity (e.g., Ehrlich and Ehrlich 1981, Prescott-Allen and Prescott-Allen 1983, 1986, Norton 1986, Wilson 1988, World Wildlife Fund 1991). The value of biodiversity is our fundamental assumption. If we did

not believe in it, we would not be writing this book. However, it is worth reviewing briefly the types of value that humans ascribe to nature. Often arguments about what is proper management of natural resources can be put in perspective, if not totally resolved, by understanding how people value nature in different ways. The limitations of different value justifications for saving nature also need to be understood. Although we prefer to think that nature has essentially one value—with no necessary distinction between utilitarian and intrinsic—we partition this value below for purposes of discussion.

Direct Utilitarian Values

The kind of value easiest to appreciate, for many people, is the utilitarian or instrumental value of a species or other natural resource. That the "what good is it" question is so often asked suggests that many people value things largely for their direct utility for humans. Though incomplete as a justification for saving biodiversity, such values are real.

The medicinal value of certain plants and invertebrates provides a powerful argument for conservation, as does the value of wild gene pools for agriculture and wild populations for food. Wild species provide an estimated 4.5 percent of the Gross Domestic Product of the United States, worth $87 billion annually in the late 1970s (Prescott-Allen and Prescott-Allen 1986). Fisheries contributed 100 million tons of food to people worldwide in 1988 (FAO 1988). One-fourth of all prescription drugs in the United States contain active ingredients extracted from plants, and nearly 3000 antibiotics are derived from microorganisms (WRI, IUCN, UNEP 1992). These statistics suggest that it is in our best interest to prevent extinctions of species that are potentially useful to us. What if the Pacific yew, until recently considered a trash tree and destroyed during clearcutting in the Pacific Northwest, were extinguished before we discovered that it contained taxol, a valuable new drug for treating several forms of cancer? This question is of more than academic interest. By one estimate, only about 5000 (2 percent) of the 250,000 described species of vascular plants have been screened for their chemical compounds (World Wildlife Fund 1991). We are driving species to extinction without even trying to learn what they might contribute to human society.

Arguments based on utility are limited, however. Leopold (1949) observed that "one basic weakness in a conservation system based wholly on economic motives is that most members of the land community have no economic value." Similarly, Ehrenfeld (1988) lamented, "what biologist is willing to find a value—conventional or ecological—for all 600,000-plus species of beetles?" What happens if we thoroughly screen a plant for medicinal compounds and conclude that it has none? Do we then say it is permissible to extinguish that species? Conservationists often fall into the trap of justifying species preservation for utilitarian purposes, thereby sanctioning the humanistic attitude that is responsible for the biodiversity crisis (Ehrenfeld 1978, 1988). The attitude implied by economic valuations is that the worth of a species depends on its direct ultility to humans. If a species does not benefit us, it is worthless.

At best, the utilitarian argument for biodiversity conservation is a double-edged sword. Under some circumstances it might help gain public support for protecting species and ecosystems, but in other cases it can be used to justify destruction of seemingly worthless forms. In all cases, it encourages disrespect for species in and of themselves. Thus, we are troubled that current arguments for maintaining international biodiversity, such as those expressed in the Global Biodiversity Strategy produced by the World Resources Institute (WRI), World Conservation Union (IUCN), and United Nations Environment Programme (UNEP) (1992), are thoroughly utilitarian; they hinge almost entirely on presumed benefits to humans. The sustainable development theme of the Global Biodiversity Strategy and related international conservation programs is potentially dangerous. Sustainable development could do more harm than good to biodiversity if strict protection of sensitive areas is not part of the program (Robinson 1993).

Indirect Utilitarian Values

Natural ecosystems and biodiversity also provide benefits to humans that are indirect, yet essential. Paul and Anne Ehrlich (1981) call these benefits "ecosystem services." Every habitat on Earth, including urban and agricultural environments, is an ecosystem that receives and transforms energy, produces and recycles wastes, and relies on complex interactions among species to carry out these functions. But urban and agricultural ecosystems are dependent on natural ecosystems for their sustenance. Solar energy is the basis of virtually all food chains (rare exceptions include chemically based communities in deep-sea vents) and is converted to chemical energy by photosynthetic plants. Plants, including crops, often depend on animals to pollinate their flowers and disperse their seeds, on nitrogen-fixing bacteria to convert molecular nitrogen to a form that can be assembled into proteins, and on microorganisms to convert complex organic compounds into inorganic nutrients that can be taken up by their roots. Animals, fungi, and microbes in an ecosystem have comparable interdependencies. Thus, an ecosystem is a richly interconnected web of relationships greater than the sum of its parts.

But how does a natural ecosystem benefit humans, besides providing pharmaceuticals and other products? An entire book could be written on this subject. Ehrlich and Ehrlich (1981) describe ecosystem services upon which human civilization is entirely dependent, including: (1) maintaining atmospheric quality by regulating gas ratios and filtering dust and pollutants; (2) controlling and ameliorating climate through the carbon cycle and effects of vegetation in stimulating local and regional rainfall; (3) regulating freshwater supplies and controlling flooding (wetlands, for example, can act as giant sponges to soak up moisture during rainy periods and release water slowly during dry periods); (4) generating and maintaining soils through the decomposition of organic matter and the relationships between plant roots and mycorrhizal fungi; (5) disposing of wastes, including domestic sewage and wastes produced by industry and agriculture, and cycling of nutrients; (6) controlling pests and diseases, for example through predation and parasitism on herbivorous insects; and (7) pollinating crops and useful wild plant species by insects, bats, hummingbirds, and other pollinators.

The public-service functions of ecosystems remain little known to most people, perhaps because we need to understand ecology in order to appreciate the functional relationships that underlie these services. Our society, by any measure, is ecologically ignorant. The role of biodiversity in supporting ecosystem services is striking, but we cannot easily predict how many or what kinds of species can be lost before ecosystems break down. Because all ecosystems contain some functional redundancy (with different species playing similar roles), we might impoverish an ecosystem substantially before impairing basic ecological processes such as nutrient cycling. From a ultilitarian perspective, we don't *need* every species. Some simplified, human-created ecosystems may perform virtually all of the public service functions reviewed above. The danger is that natural ecosystems have evolved their functional relationships over thousands or millions of years, whereas our experiments in manipulating ecosystems are comparatively brief. Who knows when we may lose a species or set of relationships critical to ecosystem function?

Recreational and Esthetic Values

Probably most people who care about the environment are motivated primarily by their personal appreciation of nature's beauty. John Muir, founder of the Sierra Club and a leading force in the creation of the U.S. national park system, firmly believed that exposure of ordinary people to wild places would foster an attitude to save these places (Fox 1981). Leopold (1949), too, noted that people will behave ethically only toward something they can experience and have faith in. Recreational and esthetic enjoyment of nature often leads directly to appreciation of nature for its own sake, that is, to a spiritual or ethical appreciation of biodiversity. Without people motived by their experiences of wild places, we would arguably have fewer wild areas remaining and the status of biodiversity in North America would be even more precarious.

Despite the critical role of these kinds of human experience in promoting conservation, areas set aside to fulfill recreational or esthetic objectives do not necessarily meet biodiversity conservation goals. Many national parks, wilderness areas, and other large reserves selected on the basis of esthetic criteria are relatively depauperate biologically. The Forest Service evaluates the "need" for wilderness designation on the basis of expected recreational visitor days, not on biological criteria. As a result, most wilderness areas are rock and ice, or other such scenic but not particularly diverse lands.

Many managers of national forests and other public lands, forced to reduce commodity production because such uses were unsustainable and in violation of environmental laws, are turning to recreation as an alternative use of these lands. This trend can be risky to the extent that it emphasizes motorized recreation. Managers justify road-building, leaving logging roads open to the public, and allowing use of off-road vehicles by arguing that the public needs access to these lands. Motorized recreation is almost always destructive of biodiversity. Furthermore, it encourages an attitude of dominance over nature. As Leopold (1949) put it: "It is the expansion of transport without a corresponding growth of perception that threatens us with qualitative bankruptcy of the recreational process. Recreational development is a job not of building roads into lovely country, but of building receptivity into the still unlovely human mind."

Thus, conservation arguments based on promoting human enjoyment are incomplete, at best. A deeper reason for protecting nature must be found.

Intrinsic, Spiritual, and Ethical Values

The limitations of utilitarian arguments for conserving biodiversity leave an alternative: the appreciation of wild creatures and wild places for themselves. We believe that nature and biodiversity possess *all* the kinds of value reviewed above, but that intrinsic values (or the spiritual and ethical appreciation of nature for its own sake) offer the least biased and ultimately most secure arguments for conservation. Virtually all religious traditions recognize the value of a human being—for example, a newborn baby—as at least partially independent of what that person might do for us. Why shouldn't we feel the same way about other creatures? The acknowledgment that natural objects and processes are valuable in themselves reflects a basic intuition of many people. Science cannot prove or disprove intrinsic value. Yet as scientists, we see no objective reason for believing that humans are fundamentally superior to any other organism. If we have value, then all natural things have value.

The ethical basis for respecting and protecting nature was expressed eloquently by Aldo Leopold (1949) in his famous essay on the land ethic. "A thing is right," Leopold wrote, "when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise." Ecologists might quibble with Leopold's choice of such imprecise terms as integrity and stability, noting that Nature is instead dynamic and unpredictable (Botkin 1990), and they might wonder how we can objectively measure beauty. But few challenge his primary message that ethical obligations must encompass more than our fellow human beings (Nash 1989, Noss 1992a). Many philosophers have joined Leopold in calling for consideration of all life in our decisions about what is morally right or wrong (Devall and Sessions 1985, Rolston 1988, Naess 1989). To do so is to expand our circle of ethical concern beyond the individual self and ultimately to the ecological self—the land as a whole (Fig. 1.4).

Without moral consideration of the needs of other creatures, policies for protecting biodiversity remain on shaky ground. Thus, we urge a reaffirmation of the World Charter for Nature, adopted by the United Nations General Assembly in 1982, which stated: "Every form of life is unique, warranting respect regardless of its worth to man, and, to accord other organisms such recognition, man must be guided by a moral code of action."

Where Have We Failed?

The United States has a long and venerable conservation history, with many accomplishments worthy of pride. Our laws, including the National Park Organic Act of 1916, the Wilderness Act of 1964, the Endangered Species Act of 1969 and 1973, and the National Environmental Policy Act of 1969 and 1973, are held up as models for the world to follow. Yet the biodiversity crisis continues to worsen. Our air and water get dirtier, the ozone layer thins, and most significantly for biodiversity, more and more natural habitat is destroyed in the name of progress and jobs. Why have the American people allowed this to happen?

Let us briefly examine the failure of conventional conservation practices and institutions to address the "big picture" (this topic will be explored in

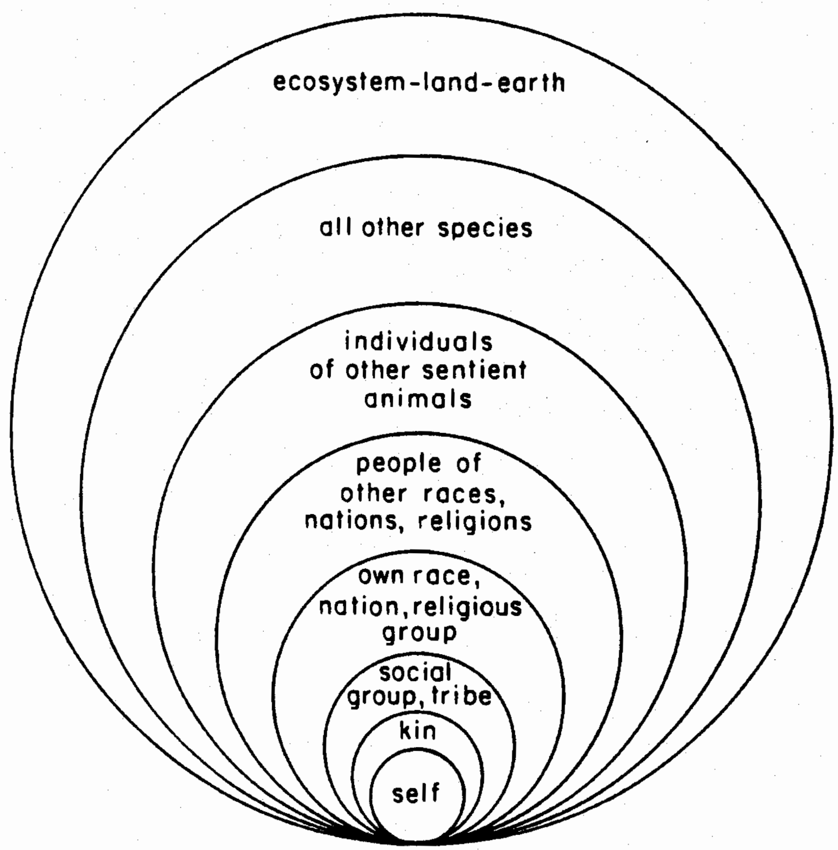

FIGURE 1.4 An ethical sequence, showing circles of moral concern and obligation increasing from the self and immediate family to all other species and the earth as a whole (the ecological self). Concern for higher levels is an extension, not a replacement, of traditional ethical concern for human beings. From Noss (1992a). Used with permission of Routledge, Chapman & Hall.

more depth in Chapter 3). We have laws, regulations, and agencies set up to protect aspects of the environment, yet none of them has measured up to the challenge of protecting biodiversity as a whole. We have trained four generations of professionals in forestry, wildlife management, fisheries, and range conservation, yet these disciplines remain fragmented and are often narrow. The traditional approach to conservation has been piecemeal: species by species, resource by resource, project by project, threat by threat.

The first laws in the United States oriented toward natural resources were game protection laws. Market hunting was big business in the late nineteenth century. After George Perkins Marsh (1864) published *Man and*

Nature, wildlife declines became widely recognized. Sportsmen led the fight to enact more laws protecting wildlife, including a bill outlawing bison killing in 1874, pocket-vetoed by President Grant for anti-Indian reasons; the Lacey Act (1900), authorizing the federal government to prohibit interstate transport of illegally taken game and wildlife parts; and the Migratory Bird Treaty with Canada (1916) and Mexico (1936), which protected nongame birds. Meanwhile, the Boone and Crockett Club was established in 1887, largely to promote sport over market hunting, and The Audubon Society was formed in 1886 to combat the fashion of wearing the feathers and skins of birds.

About the same time, Americans began formally protecting places where wildlife and scenery could be enjoyed. The Yellowstone Park Protection Act passed in 1892, twenty years after actual creation of the Park. Yellowstone and other national parks were not established primarily to protect wildlife, but rather "to conserve the scenery and the natural and historic objects and the wild life" within parks, and "to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations" (National Park Organic Act of 1916). Also in 1892, the Sierra Club was founded by John Muir and other mountain hikers (Fox 1981). The first federal wildlife refuge, Pelican Island, Florida, was established by Theodore Roosevelt in 1903 to protect egrets, herons, and brown pelicans from plume hunters. Before leaving office in 1909, Roosevelt created 51 refuges for birds and mammals (Zaslowsky 1986), but he also escalated the war against wolves, bears, puma, and other predators (Worster 1977).

Conservation history in the United States is largely a series of responses to urgent threats against popular species and scenic wonders. Game management rose as a formal science in the United States in the 1930s, with the publication of *The Bobwhite Quail* by Herbert Stoddard (1931), and *Game Management* by Aldo Leopold (1933), and with the founding of The Wildlife Society in 1937. Most of wildlife management since then has been concerned with promoting population surpluses of favored species. Some single-species projects have worked remarkably well. The intended beneficiaries, game species like the wild turkey and endangered species like the peregrine falcon, have made remarkable comebacks as a result of reintroductions and intensive management. But such management has cost millions of dollars per species. Efforts this expensive can hardly be applied to all species. Even if such enormous funds were available, the conflicting needs of different species would make management inefficient and conflict-ridden.

Many biologists now acknowledge that, despite notable successes, single-species management has caused many problems. For instance, game managers traditionally advocated forest harvest patterns that maximized fragmentation of the landscape because many game species thrive where forage and cover areas are interspersed and edges between habitat types are abundant (Leopold 1933). But we now know that while fragmentation may benefit deer and other game, it does not contribute to native biodiversity (Noss 1983). Forest fragmentation has benefited deer so much in the upper Midwest that several conifer species are not regenerating in many areas due to overbrowsing (Alverson *et al.* 1988). Intense herbivory from white-tailed deer threatens many rare plant species throughout the eastern and midwestern United States (Miller *et al.* 1992). In addition to manipulative habitat management, control of predators for the benefit of game animals and domestic livestock has led to many ecological problems (Dunlap 1988). Amazingly, costly and destructive predator control continues on public lands today.

When wildlife managers expanded their concern beyond game species and began considering nongame and endangered species, the circle of conservation broadened. Leopold (1933) recognized a historical and progressive sequence of wildlife management: (1) restriction of hunting, (2) predator control, (3) reservation of game lands, (4) artificial replenishment, and (5) environmental controls. Environmental control is habitat management and is based on ecological principles and empiricism. As acknowledged by Leopold, this approach has considerable potential for expansion to nonhunted species. But the spectrum of species considered by most conservation programs today remains limited.

Endangered species efforts, by definition, do not worry about life forms until they teeter on the brink of extinction or appear to be rapidly approaching that brink. A recent study found that 39 plant species in the United States were listed only when 10 or fewer individuals were known to exist; a freshwater mussel, *Quadrula fragosa*, was not listed until a single nonreproducing population remained (Wilcove *et al.* 1993). Because we wait so long to list species, saving them is bound to be expensive and the chances of success are poor. Most of the funding for recovery of listed species has been devoted to a few popular vertebrates (Kohm 1991), and even then recovery targets are usually less than what it would take to restore population viability (Tear *et al.* 1993).

Endangered species programs, although critical as a safety net to catch imperiled species where other actions fail, are obviously reactive rather than proactive. They make no attempt to identify potentially vulnerable species before they begin the slide toward extinction. They usually fail to recognize opportunities for protecting suites of species, such as those associated with an endangered ecosystem type, in a cost-effective way. They pay no attention to levels of organization beyond species. Although the first stated purpose of the Endangered Species Act of 1973 is "to protect the ecosystems upon which endangered species and threatened species depend," the agencies have never taken this ecosystem protection mandate seriously, and Congress has never told them how they might do so.

Nongame species programs have the potential to be proactive and taxonomically broad, but with very few exceptions (states such as Missouri, which has a portion of its sales tax allocated to conservation) they have received little funding. Furthermore, their focus has usually been on vertebrate groups popular with the public, such as birds, and they have made little attempt to determine the conservation needs of such groups as salamanders, mites, liverworts, or fungi. Because there has been no effective national nongame program, state programs operate without full knowledge of what is going on around them and have little incentive or opportunity to coordinate programs with other states and nations.

The continually expanding list of endangered species and ongoing degradation of entire ecosystems is proof enough that current approaches to conservation are flawed. In the case of the Endangered Species Act, grossly inadequate funding and political interference with listing and recovery actions are much to blame (Bean 1991). But today the Endangered Species Act and other conservation laws are being asked to do more than what they were designed to do. Knowledge of conservation problems and techniques has expanded greatly since these pieces of legislation were enacted. The interdisciplinary field of conservation biology is growing at a phenomenal pace. And, hopefully, our esthetic and ethical appreciation for life has deepened since the early days of American conservation.

Many conservationists now insist that we move beyond game species, endangered species, and other popular organisms, and start inventorying and protecting whole assemblages of species, habitats, and ecosystems before they decline further. What's more, the grassroots members of the "New Conservation Movement" (Foreman 1991) are urging ecological restoration at a massive scale, including removal of roads and developments in many areas and reintroduction of large predators. Dissatisfied with a biologically simplified America, they want back much of what has been lost.

And why not? At first glance, a vision of North America with regained wildness and biodiversity seems unrealistic, even utopian. But when we consider that restoration at this scale is a process requiring decades or even centuries, it begins to make sense (Soulé 1992). Perhaps recovery is inevitable. The human population cannot grow forever, and must either plateau, decline gradually, or crash. In any case, repairing the damage our culture has done and giving other creatures a fair chance for life is the job of enlightened management today and in the future. This is our chance to pay retribution.

Why Management?

Throughout this book we use the term *management.* All land management is biodiversity management, whether intended or not. All land-use decisions—including a decision to designate a reserve, put a fence around it, and leave it alone—are land management decisions with significant consequences for biodiversity. It is much better to manage biodiversity by design rather than by default. As the most powerful species on earth, we can alter biodiversity worldwide and are expressing that capability in a frightening way. Accepting responsibility for our actions means not only that we carefully consider the effects of management on biodiversity, but also that our management programs be designed explicitly to protect and restore native biodiversity.

In some respects, management is an arrogant concept. How can we presume to manage nature if we can't even manage ourselves? What right do we have to manage and manipulate landscapes for human ends, be they conservation or development? Why not let landscapes manage themselves and let organisms fulfill their evolutionary destinies with little human interference? We are sympathetic to these concerns but believe that, for better or worse, humans are now responsible for the continuing or ending of 3.5 billion years of organic evolution. Such power must be wielded carefully and wisely.

Land managers often become overly enthusiastic and manipulate habitats that should be left alone. On the other hand, stopping land management would in many cases be an ecological disaster. In landscapes already fragmented by human activity, the remaining natural areas are vulnerable to all sorts of threats from outside their boundaries, including edge effects. For example, the brown-headed cowbird, a parasite that lays its eggs in the nests of other birds, may need to be controlled if other bird species are to survive in remaining patches of forest. Management of the endangered Kirtland's warbler and black-capped vireo includes trapping and removing cowbirds. Without such intrusive management, these endangered birds cannot reproduce successfully. Exotic plants, such as Japanese and bush honeysuckles in eastern forests and kudzu in the South, often seriously compete with native species and need to be controlled. Without management, invasive exotics overrun many landscapes and eliminate some native species. In all such cases, we have created a dangerous situation—an environment favorable to proliferation of weedy and exotic species—that we must now correct

through management or risk losing more biodiversity as sensitive species decline.

Vegetation types that require frequent fire to maintain their native species composition and structure offer some of the strongest arguments for ecologically informed management (see Chapter 2). A small, isolated patch of prairie in a fragmented landscape is not likely to receive lightning strikes often enough to burn regularly and sustain its natural structure. If we do not manage these fire-dependent systems by use of prescribed fire, they will lose their native biodiversity.

The role of management in conservation strategy can be denied only at great risk. But perhaps management is optimally a set of interim measures that will help ecosystems recover their natural values. The ideal future may be one where management is no longer needed because ecosystems are wild and healthy enough to take care of themselves. Even if one does not accept this long-term goal, it cannot be denied that large, essentially self-managing wilderness areas are among the most important reservoirs of native biodiversity today. No one really knows how to manage a natural ecosystem. Thus, "we should at least keep our minds open to the proposition that nature—if given a chance—can still manage land better than we can" (Noss 1991b).

We fear, unfortunately, that letting things be is not a safe option for much of our landscape in the near future, however valuable it may be as a guiding principle for large wilderness areas and possibly for some distant future worldwide. But concerning management, one thing is clear: Traditional approaches have failed to protect biodiversity. A new approach to land conservation, built on what we feel is the best of past and current approaches, is developed later in this book. But first, we examine in more detail the forces responsible for evolution of biodiversity in North America and the limitations of past approaches to managing this incredible diversity.

CHAPTER TWO

BIODIVERSITY: CREATION AND DESTRUCTION

> Our place is part of what we are. Yet even a "place" has a kind of fluidity; it passes through space and time...A place will have been grasslands, then conifers, then beech and elm. It will have been half riverbed, it will have been scratched and plowed by ice. And then it will be cultivated, paved, sprayed, dammed, graded, built up. But each is only for a while, and that will be just another set of lines on the palimpsest. The whole earth is a great tablet holding the multiple overlaid new and ancient traces of the swirl of forces. Each place is its own place, forever (eventually) wild.
>
> Gary Snyder (1992), *The Practice of the Wild*

During a recent interagency course on biodiversity, we posed a set of questions to land managers about the habitats and species they were charged with managing. Our questions included "When were the present plant communities formed in geological time?"; "What were climatic conditions like then?"; "What species were present then that are absent now?"; and "What ecological processes are responsible for maintaining the biotic community?" Referring to particular species in the habitats that course participants were managing, we asked "Where did the species originate or evolve?"; "What were environmental conditions like there?"; and "How do current conditions compare with conditions under which the species evolved?" Answers given by managers to both sets of questions were often less than satisfactory. Perhaps these questions seem academic and of little relevance for on-the-ground managers, who must deal with present conditions and immediate "brush fires." However, failure to address such questions has led to some regrettable resource management decisions. It is comparable to practicing medicine without taking patient histories or understanding anatomy or physiology.

To devise practical methods to conserve biodiversity, biologists and managers need to understand (1) the geological and evolutionary forces responsible for generating biodiversity, (2) the ecological processes that maintain biodiversity, and (3) the forces that threaten biodiversity. This understanding is needed whether dealing with the gene, species, ecosystem, or landscape level, and whether management focuses primarily on biodiversity conservation or on something else, such as wildlife, timber, or livestock production.

Land managers have made mistakes because they did not understand or consider biogeographic and ecological factors. For example, giant sequoias found only in the southern Sierra Nevada of California are geological and successional relicts dependent on recurring fire for persistence (Harvey *et al.* 1980). Silvicultural practices developed for expanding, widespread, or late-successional tree species have not worked for sequoias. Similarly, range managers have applied management principles from the Great Plains, where plant communities evolved in the presence of large herding herbivores, to Great Basin and southwestern desert areas, which had no such fauna for thousands of years.

Managers also need to understand better the processes that are threatening biodiversity. In many cases, knowledge of factors that shaped or maintained a biotic community will provide clues to current threats. If some process critical to the life histories of native species is disrupted, biodiversity can be expected to decline. For example, trout and salmon (Family Salmonidae) need clean gravel beds for spawning. These beds are maintained by periodic high water in streams, termed "flushing flows." Dams, water diversions, and excessive soil erosion from logging or road building can reduce the frequency and effectiveness of flushing flows, and cause a decline in salmonid populations.

In this chapter we review some major forces that have created, shaped, and maintained the biodiversity of North America and some other forces that now threaten it. Though brief and general, our review highlights some types of knowledge required to develop effective conservation plans and programs.

Generation of Biodiversity

Before outlining the forces responsible for shaping biodiversity in North America, we must discuss how biological variation develops. This discussion assumes some knowledge of evolutionary theory and is not intended to be a primer; readers lacking such background may wish to consult a general biological text or one of the many popular books that deal with the subject, such as Ehrlich (1986).

Evolution

Ever since Darwin's exposition of the theory of evolution by natural selection in *The Origin of Species*, biologists have devoted much effort to elucidating the finer points of how this process works. Despite continuing disagreement about aspects of evolution, such as whether speciation proceeds at an even pace or in bursts, modern evolutionary theory is adequate to explain the general processes by which variation among organisms has developed. Since we have stated that biodiversity can be conveniently recognized at four levels (gene, species, community, landscape), let's consider how variation develops at each of these levels.

1. Variation within a species results ultimately from mutation and recombination of genes. Since certain genes confer a competitive advantage in a given environment, individuals having these genes will more successfully survive and reproduce (i.e., natural selection for these genes has occurred). If a species has colonized many different areas, it may develop genetic differences among populations due to selection for genes best adapted to each particular habitat. For example, populations living in drier habitats may develop physiological or behavioral adaptations (such as concentrated urine or nocturnal activity) to conserve water. Thus, variation among populations of the same species is often a function of the diversity of habitats that the species occupies across its range.

Of the countless examples of natural selection, some patterns are common enough to have been codified into rules of thumb. For example, Bergman's rule states that individuals in northern populations of endothermic ("warm-blooded") species are larger than those in southern populations, presumably because larger bodies have lower surface–volume ratios and thus better conserve heat. Hence, moose in Alaska are predictably larger than moose in Yellowstone National Park. Similarly, populations of many plants and animals vary in shape and color across their range. Sometimes the adaptive value of a trait can be explained scientifically and sometimes it cannot. For example, the northern flicker, a common woodpecker, has yellow under its wings in the eastern United States but salmon color in most of the West. Why? No one knows for certain. Some traits may not be adaptive; instead, they may be genetically linked (e.g., close together on the same chromosome) to traits that are adaptive, or they may represent examples of neutral evolution or random changes in gene frequencies (genetic drift) that often occur in small, isolated populations.

2. New species arise when populations diverge genetically (and often, physically) and are no longer able to interbreed, at least in the wild. Reproductive isolation can evolve in several ways, and usually follows the physical isolation of populations by geographic barriers such as rivers, glaciers, or mountain ranges. For example, mountain sheep of the genus *Ovis* were separated by Pleistocene (Ice Age) glaciation and evolved into the thin-horned Dall sheep in Alaska and Canada and the bighorn sheep to the south (Geist 1971). Several bird species, including warblers, also may have arisen when glaciers separated ancestral populations. Similarly, the eastern and western diamondback rattlesnakes were apparently the same species until some time during the Pleistocene when populations in southeastern and southwestern refugia became isolated and differentiated into distinct species (Futuyma 1979). Any physical or topographic feature that prevents movement by plants or animals can isolate populations and allow new species to evolve. Alternately, isolation can lead to extinction if the isolated populations are too small.

Island Biogeography

Islands are inherently surrounded by barriers and many islands have floras and faunas that differ drastically from the continental areas with which they are associated. For example, the Channel Islands off the coast of California have approximately 100 species of endemic plants (Davis 1990). Endemic species or races are ones that are native to a particular place and found only there. Beginning with Charles Darwin's trip to the Galapagos Islands, much of our understanding of evolutionary processes has come from the study of islands.

The species–area relationship, first noted with respect to islands, is one of the great empirical generalizations of biogeography. As the area of any habitat declines, so does the number of species. Johann Reinhold Forster, naturalist on Captain Cook's second tour of the Southern Hemisphere in 1772–1775, noted that "islands only produce a greater or lesser number of species, as their circumference is more or less extensive" (cited in Browne 1983). Later studies confirmed the species–area effect for oceanic islands and extended the effect to habitat islands such as caves, isolated wetlands, alpine grasslands, and forest fragments. Typically, a tenfold decrease in habitat area cuts the number of species by half (Diamond 1975).

What are the causes of the species–area relationship? Scientists have long argued over this question. The most straightforward explanation in many cases is habitat diversity. As area increases, so does the diversity of physical habitats and resources, which in turn support a larger number of species (Lack 1976). Imagine a large oceanic island containing desert, montane forests, streams, and marshes. A volcano erupts and annihilates all living space on the island except part of the desert, which contains few of the species that lived in the other habitats; diversity has been reduced accordingly.

Abundant evidence supports the generalization that larger populations have a smaller chance of going extinct. A small island or nature reserve may not contain enough area for a single home range of a large animal. For example, a grizzly bear will not find enough to eat for long in a reserve of a few thousand acres. Other species, for reasons not entirely understood, avoid settling in small tracts of forest or other seemingly suitable habitat. Studies in the eastern United States have confirmed that many songbirds are area-sensitive and breed only in large tracts of forest, even though their individual territories consist of only a couple acres (Whitcomb *et al.* 1981, Robbins *et al.* 1989). Random factors may be partially responsible for the species–area relationship; the more individual plants or animals sampled by a researcher, the more species that sample will contain just by chance (Connor and McCoy 1979). The odds of finding species with low population densities increase as more area is sampled.

The most famous and controversial explanation for the species–area relationship is the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967). MacArthur and Wilson proposed that the number of species on an island represents a balance between immigration (or colonization) and extinction (Fig. 2.1). Over time, species on an island continually go extinct, but other species immigrate to the island from the mainland or other islands. Islands near the mainland experience higher rates of immigration than remote islands because the dispersal distance is shorter. Large islands contain larger populations and consequently suffer lower rates of extinction. Island size may affect immigration rates as well, as larger patches will be easier for dispersing individuals to locate. Islands close to an immigration source may also have lower extinction rates, as small populations can be augmented by immigrants of the same species, a so-called "rescue effect" (Brown and Kodric-Brown 1977). Therefore, equilibrium theory predicts that large, close islands will contain the most species, all else being equal.

MacArthur and Wilson (1963, 1967) elaborated many mechanisms related to island biogeography, and later studies have tested and refined these postulates. Much of this work may seem academic and without practical application, but many of the mechanisms proposed have turned out to be useful in understanding the process of extinction and how to prevent it.

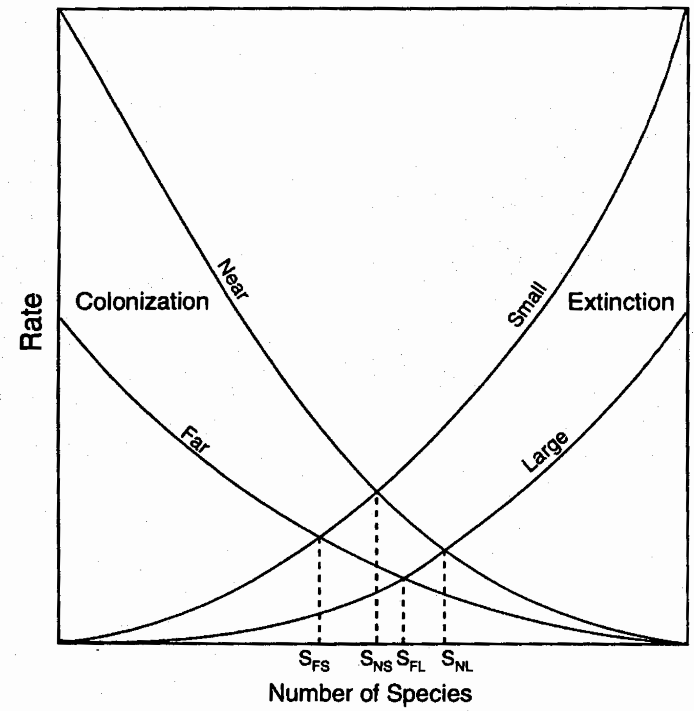

FIGURE 2.1 Predicted species richness on an island, represented as a balance between rate of colonization (immigration) to the island and rate of extinction, according to the equilibrium theory of island biogeography (MacArthur and Wilson 1967). In this model, colonization is affected mainly by island distance from the mainland (near or far); extinction is affected by island size. Species richness corresponds to the intersection of the colonization and extinction curves. The greatest number of species is predicted to occur on islands that are near and large (S_{NL}). From Wilcox (1980). Used with permission of Sinauer Associates.

INTERRELATIONSHIPS

As plants and animals colonize and adapt to new environments, relationships may develop in which two or more species interact to their mutual benefit. Certain insects have evolved to pollinate only a specific plant. Plants have evolved that depend on only one or a few species of animals to disperse their seeds. Some microorganisms have adapted to life in the gut of animals, where they digest cellulose to the mutual benefit of themselves and their host. These relationships can become quite intricate. For example, biologist Chris Maser (1988) describes the complex relationship between the northern flying squirrel and mycorrhizal fungi and their overall role in maintaining the health of the forest ecosystem in which they live. The squirrels feed on the fruiting bodies (mushrooms and truffles) of mycorrhizal fungi that trees depend on for obtaining soil nutrients through their roots. When the squirrels defecate, the fungal spores are dispersed from tree to tree. Many biologists make their living trying to sort out and understand these interdependencies. However, the documented relationships represent only a few well-studied cases. Millions of such relationships remain unknown.

The existence of mutualistic relationships and other interdependencies has led some ecologists to suggest that the biotic community is a holistic organism that is more than just the sum of its parts. However, we now know that the parts are interchangeable to a degree. Communities change in composition over space and time as species respond individually to climate and other changes. This is not to say that relationships are unimportant, but only that their nature is forever dynamic.

The Landscape Perspective

Finally, we can extend our view of how biodiversity is generated to a landscape level. A regional landscape usually consists of many different plant communities with associated animals. But these communities shift in their position on the landscape over time. Consider the northern Great Plains, which is dominated by tall grasses like big bluestem and short grasses like blue grama. For thousands of years, millions of bison traversed this region in large herds, grazing and trampling down areas to bare dirt well mixed with manure. Areas that were periodically denuded would be quickly colonized by invader plants such as fringed sagebrush that can effectively use the nutrients released into the soil. Prairie dogs would also move into these areas. Large animals such as pronghorn antelope, attracted to disturbed areas to forage, helped disperse seeds of invader plants into these areas. Over time, the flora and fauna of a disturbed site would change in a more or less predictable pattern until eventually tall grasses dominated again. This pattern of systematic replacement of biotic communities, called succession, is familiar to all foresters, range managers, and wildlife biologists. However, the end point of succession is not as predictable as once thought, particularly in times of rapid climate change. Succession also involves an element of chance, especially with regard to which species get to a disturbed site first.

The Great Plains example provides a few lessons for land managers about landscape ecology. First, disturbance and the subsequent pattern of plant and animal succession is a natural process that helps maintain long-term

ecological health by recycling or importing nutrients and invigorating soils. Second, disturbed sites depend upon surrounding areas for recovery. When a patch of grassland is denuded, adjacent areas with early successional species provide the seed sources that allow colonization by new plants. Later, adjacent mature tallgrass communities provide the supply of seeds and animals to return the area to a tallgrass stand.

Thus, community diversity within a regional ecosystem is not only a function of topographic or landform diversity but also a function of natural disturbance cycles. These disturbance cycles may be generated by the activities of animals or by climatic or geological events such as fire, flooding, landslides, or volcanic activity. In any case, they are unending.

Geologic and Biogeographic Forces

At an even broader scale, environmental change is eternally creating new expressions of biodiversity. Six major forces have had a profound effect on the current patterns of biodiversity in North America: plate tectonics/continental drift, uplift/erosion, inundation, catastrophes, climate change/glaciation, and biological invasions.

Plate Tectonics/Continental Drift

Approximately 250 million years ago all the present continents were joined together into a single giant continent, called Pangaea. Then about 200 million years ago, in the Cretaceous period, the continents began to separate into Laurasia in the north and Gondwanaland in the south. Eventually North America split off from Eurasia and formed a separate continent. Florida, however, seems to have been a part of Africa that later became attached to North America.

Continental drift isolated many life forms from each other and led to the development of distinct floras and faunas on each of the continents. Geological forces related to the shifting of continental plates also helped create a variety of habitats on each continent, including marine shelves, mountain ranges, freshwater rivers, and lakes.

Uplift/Erosion

The drift of continents has been accompanied by geological uplift, both from pressure ridges created when plates are pushed against each other and from volcanism. Pressure ridges were the major factors that uplifted most mountain ranges of the continent—the Cascade/Sierra Nevada, Rocky Mountains, and Appalachians. Uplift in each case was followed by erosion, creating the pattern of mountain ridges and valleys, and lakes and rivers in endless variety, depending on the erosiveness and penetrability of the substrate and the pattern of rain and snowfall.

This uplift and erosion, which continues today, created many new habitats. Plants and animals adapted to a range of elevational microclimates and to riparian and aquatic habitats associated with river and lake systems. Volcanic eruptions also created distinct habitats with steep elevational gradients and often with substrates rich in minerals.

Inundation

Accompanying continental movement and uplift were periods of inundation. About 110 million years ago much of the central plains of North America was covered by seas. Similarly, a large portion of the Great Basin was covered by a huge inland lake, Lake Bonneville, during much of the Pleistocene (between 10,000 and 2 million years ago). Most of the rivers running out of the mountains within or surrounding the Great Basin ran into this lake. Since that time the climate has become more arid, and many of these streams no longer have perennial flows. The Great Salt Lake in Utah is a remnant of Lake Bonneville, and the biodiversity of the Great Basin has been markedly influenced by fluctuations in the size and salinity of this lake and its tributaries. Similarly, Florida was covered by ocean for much of its geologic history until 25 million years ago; its highest ridges were formed originally as coastal dunes (Webb 1990). Because these ridges were often isolated from one another by seawater, they developed distinct endemic floras and some endemic animals, most evident today in the endangered Florida scrub of the Lake Wales Ridge.

Catastrophes

Scientists have found much evidence of periodic events that caused mass extinctions of species (particularly animals) across the planet. One of the most significant of these events marks the boundary of the Mesozoic and Cenozoic eras (approximately 63–65 million years ago). This event was characterized by a massive die-off of reptiles, especially the dinosaurs, and was followed by the rise of mammals. Increasing evidence suggests that this mass extinction was caused by a meteorite or comet as large as 6 miles in diameter striking the earth. According to this theory, the collision released a tremendous cloud of dust into the atmosphere, dramatically cooling the earth. Most plants persisted through this extinction event, apparently because of their seed banks. Animals, such as small mammals, that could feed on these seeds and were not too bothered by cold presumably also survived. Those without these adaptations perished.

Several mass extinctions are apparent in the fossil record, and probably also relate to ancient cataclysms. Five major events are recorded, and for each event 10–20 million years were needed for the diversity of species on earth to return to predisturbance levels. These extinctions and subsequent diversifications in new evolutionary directions helped shape the biodiversity of North America. Catastrophes on a global scale are extremely rare and have not occurred for 63 million years. However, the current wave of extinctions resulting from human activity is eliminating an estimated 27,000 species each year, making it the sixth great mass extinction in the earth's history (Wilson 1992).

Climate Change/Glaciation

Climate change has had a major effect on the structure of biotic communities. Climate has changed continuously, at one rate or another, throughout the history of the earth. Plants and animals have shifted their distributions in response to these changes. For example, during wetter times, redwoods covered large parts of the West from Colorado to the Pacific Coast. Climatic changes isolated and fragmented redwood populations and eventually led to the development of distinct species. Two relict species of redwoods remain, the giant sequoias of the western Sierra Nevada and the coastal redwoods along the north coast of California.

One of the most important climate-induced forces shaping the biodiversity of North America has been the periodic advances and retreats of continental glaciers in relatively recent times from the Pleistocene to the present. At least 22 separate cycles of glaciation have occurred in the Northern Hemisphere over the last million years (Graham 1986). Although many of these glaciations covered most of what is now Canada, Alaska, and as far south as the present-day Ohio River Valley, unglaciated areas (refugia) existed even in northern latitudes. Animals and plants that survived in these areas often evolved into distinct species, subspecies, or varieties. For example, there are several pairs of closely related bird species (northern shrike and loggerhead shrike; Bohemian waxwing and cedar waxwing, and so on) in which one member of the pair has a more northern but overlapping breeding range. In each case these pairs are believed to have descended from a common ancestor and then separated during a Pleistocene glaciation. After the ice receded, the southern species spread northward, and the northern species spread south and eastward (Pielou 1991).

Glaciation not only isolated species populations, but the advance and retreat of glaciers created many unique landforms and habitats such as glacial cirques so common in the Rocky Mountains and Sierra Nevada, moraines, eskers, and kettle holes. Furthermore, the soils in formerly glaciated areas often differ greatly from those in unglaciated zones, resulting in distinct plant and animal communities.

Climates have usually changed slowly in the past, but humans now appear to be changing the climate rapidly by increasing concentrations of carbon dioxide and other greenhouse gases in the atmosphere, as we will discuss later.

Biological Invasions

Ever since the continents separated, plants and animals have periodically invaded North America. A few seeds arrived on the wind, drifted across oceans, or were carried in mud on the feet of birds. Some small animals may have rafted across on logs or other debris. Spiders ballooned. At times major land bridges were available to aid colonization of terrestrial species. During glacial periods over the last 60,000 years, North America was connected to Asia near Alaska by an area called Beringia. This land bridge was once as wide as 200 miles and at times had a temperate climate more typical of areas further south today. Many species, including large mammals such as bison, bighorn sheep, elk, and moose, are believed to have reached North America by crossing Beringia during one of these periods of lower sea levels. All of these species have close relatives in the Old World. For example, the red deer in Europe is the counterpart of the larger American elk. These two animals are considered to be closely related subspecies.

Ultimately, the most influential of the invaders of North America were the humans who entered the continent from Asia during the Pleistocene. When and by which routes these people arrived in North America is still controversial, but the Beringian route and a coastal route through the same region appear most likely (Hoffecker *et al.* 1993). Humans probably arrived in North America at least 20,000 years ago, and probably in several waves thereafter, although the timing of these colonizations is uncertain.

More controversial is the effect of these early human invasions on biodiversity. Martin (1967, 1973) and others have postulated that aboriginal people had a major if not dominant role in exterminating many of the large mammals on the continent about 10 to 12 thousand years ago. This theory is not universally accepted, but has considerable support (Brown and Gibson 1983). Although humans occupied perhaps the entire continent at that time, they lived in relatively low densities. Nevertheless, evidence from around the world suggests that every major human colonization of a new continent or island has been accompanied by a wave of extinctions, especially of large mammals and flightless birds (Diamond 1982, 1984, Martin and Klein 1984).

The human invasion from Eurasia and Africa beginning around 1500 has had the most pronounced effect on the biodiversity of North America. Not only did these people develop population densities far higher than the continent had ever experienced, but their per capita use of resources was much higher and typically quite inefficient. Furthermore, they brought with them many organisms from Europe and Africa that became naturalized here, often with devastating effects. These exotic organisms include horses introduced into the Southwest by the Spaniards, carp introduced by German immigrants into our waterways, and the many deliberate introductions of birds such as starlings and house sparrows. Introduced species also include plants such as tamarisk, introduced as an ornamental tree from the Middle East and now spread throughout riparian areas of the Southwest; and cheatgrass, which was accidentally introduced from contaminated grain and has spread throughout most of the West. Many of these introductions have disrupted ecological processes and caused displacement of native species. In other cases, introduced species hybridized with closely related varieties or species, thereby polluting native gene pools.

Fish provide a good example of the damaging effects of exotic species on native biodiversity. Of the 1033 species of freshwater fish in North America, 27 (or 3 percent) have become extinct within the past 100 years and another 265 (or 26 percent) are vulnerable to extinction (Miller *et al.* 1989). Displacement by introduced species has been implicated as a cause of decline in 68 percent of these species, topped only by physical habitat destruction at 73 percent (the percentages add up to more than 100 because more than one cause affects most species). In addition, hybridization with other species and subspecies is listed as a cause of decline in 38 percent of species.

This pattern of displacement and genetic pollution is well documented in fishes, but is by no means unique to them. Exotic species are one of the greatest threats to native species and to human-disturbed ecosystems in the world (Reid and Miller 1989).

The introduction of exotic diseases to which native species had little or no resistance has sometimes had devastating effects. For example, domestic sheep carried diseases that when transferred to the closely related bighorn sheep of North America caused mortality resulting in local extirpation, a pattern that continues today except when domestic sheep are carefully controlled within bighorn ranges. Similarly, canine distemper, introduced in North America by domestic animals, particularly dogs, is fatal to the endangered black-footed ferret and may be partly responsible for the historic reduction in ferret numbers (Schroeder 1987).

Ecological Processes Maintaining Biodiversity

Over thousands or millions of years, biotic communities change dramatically, for instance from prairie to forest and back again. However, over shorter periods, measured in decades or centuries, many communities remain remarkably stable. In this section, we outline the processes responsible for maintaining the integrity of communities, ecosystems, and landscapes. Conserving ecological processes is essential to conserving biodiversity. Six interrelated categories of ecological processes that biologists and managers must understand in order to effectively conserve biodiversity are: (1) energy flows, (2) nutrient cycles, (3) hydrologic cycles, (4) disturbance regimes, (5) equilibrium processes, and (6) feedback effects.

Energy Flows

The flow of energy through an ecosystem is fundamental to maintaining its function. Our sun is the source of virtually all energy useful to organisms, and energy is lost continuously as it moves through an ecosystem. The most basic way in which life captures energy is through photosynthesis. Plants form the basis for food chains through which energy is passed to higher trophic levels. Any reduction in plant or leaf biomass will reduce the amount of energy flowing through an ecosystem.

Energy is captured and expended in ways other than photosynthesis. For example, solar energy evaporates water, which returns as precipitation. Upon reaching the ground, precipitation is the prime mover of physical objects in terrestrial ecosystems. Surfaces of the earth such as rock faces absorb radiant energy, and the energy from such surfaces creates a unique microsite used by many plants and animals.

Nutrient Cycles

Nutrient cycles are the processes by which elements such as nitrogen or carbon move through the biotic and abiotic components of an ecosystem. Ecosystems function by cycling and recycling; otherwise a system would eventually become depleted of essential elements or nutrients. For example, phosphorus is a nutrient that limits plant growth in many ecosystems. Phosphorus is found in certain phosphate rock formations in the earth's crust. Slowly, through weathering and erosion, phosphorus moves into rivers and to the ocean. There it forms insoluble deposits on the bottom of shallow areas near the coast, where it can eventually be uplifted. Other phosphorus settles in deep marine deposits, which for all practical purposes do not cycle back through land. Because geological uplifting is so slow, phosphorus is being washed into the sea faster than it returns to land (Miller 1982). Fish catches return 54 million kg (60,000 tons) of phosphorus each year, and the phosphorus-rich guano of fish-eating birds, such as pelicans, gannets, and cormorants, returns another 3100 million kg (350,000 tons). But these amounts are small compared to the larger amounts of phosphorus that erode from the land to the oceans each year.

The cutting of forests and other land clearing accelerates natural erosion losses.

Conversely, elements or compounds that cannot be cycled will accumulate somewhere in the ecosystem and may cause toxicity. Pesticides such as DDT, which are not natural components of an ecosystem, are neither metabolized nor detoxified as they pass through the ecosystem and tend to accumulate in toxic proportions in the fat of animals high in the food chain. DDT is proven to have caused declines in animal populations. DDT and other chlorinated-hydrocarbon pesticides concentrate in tissues of peregrine falcons and other predatory and fish-eating birds and can cause eggshell thinning, behavioral abnormalities, and other problems resulting in reproductive failure. The decline of peregrine falcons in North America and their subsequent recovery are closely correlated with prevalence of DDT in the environment and in the bird tissues (Craig 1986). Populations and northern subspecies that were not exposed to pesticides did not decline as did more southern populations.

Of particular importance in nutrient cycles is the role of decomposers. Ecologists often focus on the food chains of plant–herbivore–carnivore since this is the most visible part of a nutrient cycle to us. However, without the invertebrates and microorganisms that decompose and recycle dead material at each stage, the world would soon be without soil nutrients to feed the plants that capture the sun's energy. And there would be lots of dead bodies lying around.

Hydrologic Cycles

Another process critical for life is the hydrologic cycle, the process through which water moves from ocean to atmosphere to land and back to the ocean. Water is a finite resource, renewed and regulated in complex ways. Water is necessary for all life from the molecular level through the ecosystem level. Furthermore, it is the major vehicle through which materials, both abiotic and biotic, are transferred through an ecosystem. Hence, water is a key factor in the occurrence and distribution of organisms. For example, vernal pools, containing water for only a short period of the year, often support plant species and associations not found on adjacent higher ground. Proper water cycling is critical to maintaining the biodiversity and functioning of biotic communities.

Disturbance Regimes

As noted earlier, most ecosystems are subject to regularly or sporadically recurring events such as fires, windstorms, landslides, or floods. These events are often called catastrophic, but historical records show that they have always occurred and that ecosystems have complex responses to them. What appears to devastate a natural community at a local scale or in the short term by causing death and destruction may actually be essential to rejuvenation and persistence at a broader spatiotemporal scale.

Many plant and animal species are not only adapted to disturbances, but depend on them for survival. A well-studied example is the Kirtland's warbler, which requires homogeneous thickets of five- and six-year-old jack pines interspersed with grassy clearings for breeding. This kind of habitat is created and maintained by intense fires (Lowe *et al.* 1990). If fires are suppressed, as is usually the case in managed forests, habitat for Kirtland's warbler would disappear. Restoring and maintaining a regular pattern of fires has helped conserve this endangered species.

Prairies, other grasslands, oak savannas, and ponderosa and longleaf pine forests often depend on frequent, low-intensity ground fires. These fires recurred historically at intervals of 1 to 25 years, depending on the particular community and site conditions. The life histories of the dominant species in these communities have been shaped evolutionarily by fire (Mutch 1970, Platt *et al.* 1988). Without fire, these communities gradually change to other types that may be less diverse or healthy (e.g., Walker and Peet 1983, Anderson *et al.* 1987, Habeck 1990). Most fire-dependent communities evolved in areas with frequent thunderstorms and lightning ignitions, although in some cases, burning by native Americans greatly increased the extent of the community over thousands of years (Pyne 1982). In all such cases, fire must be considered a normal and necessary part of the ecosystem.

Fire suppression, both active and passive (the latter occurs when firebreaks such as roads, clearcuts, agricultural fields, and developments prevent the natural spread of fire), has harmed fire-dependent communities. If a fire-dependent community goes too long without fire, it may accumulate so much woody fuel that a fire would be catastrophic, killing adult trees and perhaps even sterilizing the soil. Prescribed fire, designed to mimic the natural fire regime, seems to offer the best hope of maintaining natural diversity in these communities.

A knowledge of natural disturbance regimes is essential to conservation of biodiversity. Ecologists have developed theory and some evidence to suggest that species diversity will be highest at some intermediate frequency or intensity of disturbance (Fig. 2.2; Connell 1978, Huston 1979, Pickett and White 1985, Petraitis *et al.* 1989). Intermediate should not be interpreted as median. An optimal level of disturbance will need to be determined experimentally or through extensive observation for any given community. Determining what that intermediate intensity or frequency is remains a difficult problem for any community. At the landscape level, the influence of disturbance on species diversity is even more complex because many habitats and species assemblages are involved.

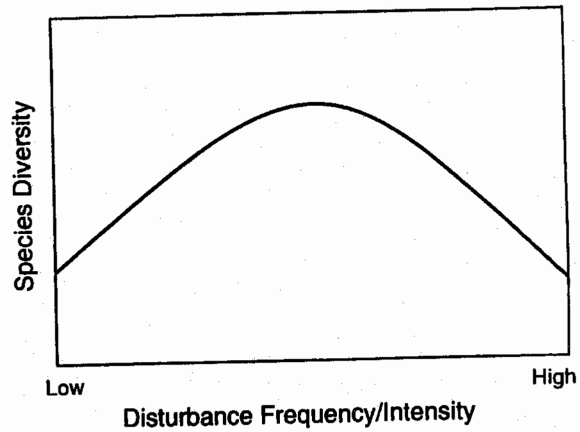

FIGURE 2.2 The intermediate disturbance hypothesis, which indicates that species diversity within a given patch should be highest at intermediate frequencies or intensities of disturbance (from Hobbs and Huenneke 1992, after Connell 1978). Used with permission of the Society for Conservation Biology and Blackwell Scientific Publications, Inc.

Perhaps more instructive for land managers is the realization that species in any region have adapted, through evolution, to a particular disturbance regime. If we radically alter that regime, many species will be unable to cope with the change and will be eliminated. For example, the patchwork created by clearcutting differs from the mosaic created by fire or windthrow in fundamental ways. A landscape of dispersed clearcuts and tree plantations—a common pattern across much of the United States—has less dead wood and other structure within patches, greater contrast between patches, and more pronounced edge effects than a naturally disturbed landscape (see Chapter 6). It also has roads and vehicles, which lead to other problems.

Human actions that dampen or eliminate natural disturbances are likely to be a threat to biodiversity in many kinds of environments. For example, many riparian plant species such as cottonwoods become established after floods, which create new deposits of bare silt and gravel where seedlings can establish. Eliminating periodic flooding by building dams may prevent regeneration of many species and drastically alter riparian plant communities.

Although disturbances are fundamentally natural, they can become unnatural and truly catastrophic when their frequency, severity, or other qualities are modified by human action. Thus, although many streams are subject to overbank flooding on the order of 100 years, an increase in frequency to every 10 years by upstream logging and grazing must be considered unnatural and potentially destructive to biodiversity. Either increases or decreases in the frequency of fire can have dramatic effects on habitat structure and species composition.

Human actions that mimic natural disturbances are much less likely to interfere with ecosystem function and threaten biodiversity than human actions that impose novel disturbance regimes on an ecosystem. Consider, for instance, livestock grazing in the northern Great Plains, which once supported bison. Restoring free-ranging bison would be the ideal management strategy from a biodiversity perspective. Short of this ideal, a livestock grazing system that mimics bison grazing patterns is more likely to be compatible with the region's remaining biodiversity than some grazing pattern based on English pasture management.

While many species and communities are well adapted to frequent disturbance, seemingly natural disturbances can still have harmful effects. In particular, they may leave communities vulnerable to invasion by exotic species, and all the inherent problems exotics cause. In an extensive review of scientific literature on disturbances, particularly on grasslands, Hobbs and Huenneke (1992) described how changing the frequency and intensity of disturbance may affect both natural diversity and susceptibility to invasion by exotics (Fig. 2.3).

Equilibrium Processes

An ecological concept of historical importance to conservation but disputed today is equilibrium. An equilibrium condition is one in which two opposite forces exist in a balanced state. For example, in many mule deer populations, birth rates roughly equal death rates, resulting in relatively stable numbers over a period of, say, 20 years. If birth rates dramatically increase without a corresponding increase in death rates, then the population would explode. If the opposite happened, the population would die out.

Equilibrium processes could potentially operate at all levels of organization: gene, species, ecosystem, and landscape. The examples shown in Table 2.1 represent only a few of many. These processes are useful to recognize because they tend to confer stability upon an ecosystem. However, not all ecosystems are stable; probably most are stable only within a limited range of environmental conditions. Modern ecological theory holds that equilibrium conditions are often fleeting and can be recognized at some spatial scales but not at others (Botkin 1990, Noss 1992a).

Feedback Systems/Homeostasis

Conventional ecological theory and resource management principles in North America have emphasized the homeostatic or negative feedback

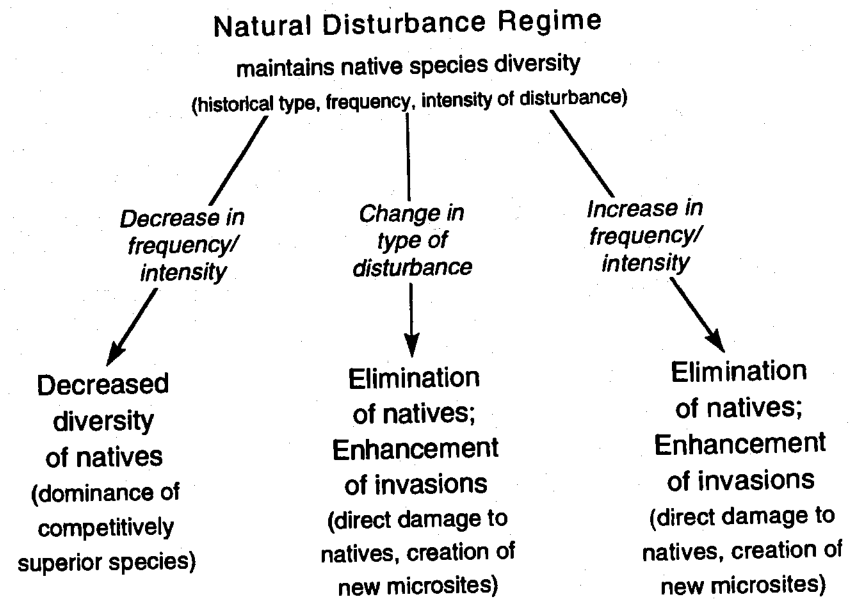

FIGURE 2.3 Any change in the historical disturbance regime of an ecosystem may alter species composition by reducing the importance of native species, by creating opportunities for invasive species, or both (from Hobbs and Huenneke 1992). Used with permission of the Society for Conservation Biology and Blackwell Scientific Publications, Inc.

processes of ecosystems. Early plant ecologists described plant succession as an orderly process by which one plant community replaces another in a predictable sequence that eventually reverts to a "climax" community. Ecosystems do exhibit some homeostatic behaviors. They tend, for instance, to respond to minor disturbances by moving back to the predisturbance state, an example of negative feedback. Controls on population size such as predation, food supply, or social behavior are also negative feedback or density-dependent mechanisms.

Negative feedback confers stability upon a system because it moves the system back toward the "original" state. For example, eastern deciduous forests that have been cleared for farming and then abandoned will revert to forests that at least superficially resemble the original ones, though they may be missing many components.

The most familiar example of a negative feedback system is a thermostat controlling the temperature of a house. When the temperature drops below the setting, the thermostat turns on the heat until the set temperature is reached. Conversely, if the house gets too hot, the thermostat will

TABLE 2.1 Potential Equilibrium Processes and Results of Disequilibrium

Level	Example	Process	Relationship	Consequences
Gene	Genetic diversity	Background mutation rate (BMR) versus rate of gene loss (RGL)	BMR > RGL	Diversification
			BMR = RGL	Genetic stability
			BMR < RGL	Loss of genetic diversity
Individual organism	Perennial plant carbohydrate reserve	Carbohydrate storage (CS) versus carbohydrate drawdown (CD)	CS > CD	Increased plant vigor
			CS = CD	Plant maintenance
			CS < CD	Decreased plant vigor; plant death
Population	Population dynamics	Birth rate (BR) versus death rate (DR)	BR > DR	Population increase
			BR = DR	Population stability
			BR < DR	Population decrease; extinction
Community	Species richness	Species immigration rate (SIR) versus species extinction rate (SER)	SIR > SER	Increased species richness
			SIR = SER	Stable species richness
			SIR < SER	Decreased species richness
Ecosystem	Nutrient balance	Nutrient import (NI) versus nutrient export (NE)	NI > NE	Ecosystem enrichment
			NI = NE	Ecosystem stability
			NI < NE	Ecosystem degradation
	Hydrologic balance	Groundwater recharge (GWR) versus groundwater discharge (GWD)	GWR > GWD	Net aquifer recharge
			GWR = GWD	Aquifer stability
			GWR < GWD	Aquifer drawdown; desertification
	Soil dynamics	Soil development (SD) versus soil loss (SL)	SD > SL	Soil buildup
			SD = SL	Soil stability
			SD < SL	Soil erosion; soil depletion
	Forest dynamics	Biomass removal (BR) versus forest growth (FG)	FG > BR	Forest succession/forest regeneration
			FG = BR	Sustained yield forestry
			FG < BR	Forest depletion; desertification

trigger the air conditioning system, which runs until the temperature drops to the desired setting. Negative feedbacks are common in nature and include the ability of mammals and birds to regulate their body temperature within a narrow range physiologically. Many ectotherms, such as reptiles, also regulate their body temperature within a narrow range, but they do so behaviorally by seeking suitable microhabitats.

Biologists and particularly resource managers tend to think of biological systems as responding to disturbance with negative feedback, thereby leading toward stability. However, recent evidence from both forests and rangelands (Archer and Smeins 1992, Niering 1987, Perry *et al.* 1989, Schlesinger *et al.* 1990) suggests that positive feedback processes that destabilize ecosystems are also important, and that ecosystems may be quite vulnerable to unusual disturbances. The implication is that if a new disturbance is strong enough or recurs with high enough frequency, the system may lose the ability to return to its original state. As a case in point, cheatgrass invaded many intermountain rangelands of the West following the introduction of livestock and overgrazing of the native bunchgrasses. Cheatgrass, an annual grass, carries fires well and can outcompete native grasses after fire. The shift from native grasses to cheatgrass has been accompanied by an increase in fire frequency, and now even with removal of the original disturbance (overgrazing), the community will not revert to perennial grass. Cheatgrass-dominated communities have become the steady state in many areas of the Intermountain West. Most ecosystems will eventually reach some relatively stable state, but in terms of biodiversity it may be a highly impoverished state.

Recognizing the potential for positive feedback in ecosystems is important, since so much theory of natural resource management (wildlife management, forestry, range management) is based on the assumption that ecosystems behave as negative feedback or self-perpetuating systems. Foresters assume, for example, that a clearcut will always return to the climax forest. Similarly, range managers have assumed that relaxation of grazing pressure will allow a system to return to climax grassland. Experience has shown that this does not always happen. Hence, we need to be more cautious in our treatment of the land.

Threats to Biodiversity

In this section we examine in more detail some major forces that threaten biodiversity. The threat to biodiversity extends well beyond the chainsaw, cows, or bulldozer that cause the immediate and visible destruction. The threat ultimately involves the fundamental tendency of our species to reproduce excessively, use resources profligately and selfishly, discount the future, and not worry about the needs of other people or (even less) other species (Soulé 1991).

ULTIMATE THREATS

The driving force behind loss of biodiversity is an increasing human population and consumption of resources. Figure 2.4 shows how overutilization of resources can lead to loss of biodiversity and extinction. The amount of resource use and magnitude of impact depends on three factors—human population size, per capita consumption, and efficiency of use:

$$\text{Resource Use} = \frac{\text{Population Size} \times \text{Per Capita Consumption}}{\text{Efficiency of Use}}$$

This relationship suggests that when aboriginal populations existed in North America in low numbers, and where individuals used few resources, the threat to biodiversity was minimal.

We are now facing an ominous situation where human populations virtually everywhere in the world are increasing. Per capita consumption is high and is being deliberately encouraged by advertising and governmental economic incentives (Durning 1992). Furthermore, efficiency of use is low because we are extremely wasteful. The result is that over 40 percent of the world's net terrestrial primary productivity is now used by humans, and the proportion is ever increasing (Vitousek *et al.* 1986).

INTERMEDIATE THREATS

The intermediate-level threats to biodiversity revolve around the way we use resources and the consequences of that use. Returning to Figure 2.4, we see that resource use or exploitation can threaten biodiversity in several ways. A complete review of intermediate threats is not necessary here; many of them, such as habitat loss and deterioration, are well documented elsewhere as they have been studied by applied ecologists for years. Others, such as the impact of roads, have been overlooked or underpublicized in many cases. Threats of importance in particular ecosystems such as forests or rangelands will be discussed in detail later. We focus now on three threats of widespread and general significance: habitat fragmentation, roads, and global warming.

Habitat fragmentation. Our understanding of the insidiousness of habitat fragmentation has increased dramatically in the last 20 years. This new understanding contradicts much of the conventional wisdom of wildlife and forest management.

Habitat fragmentation is one of the greatest threats to biodiversity worldwide (Burgess and Sharpe 1981, Noss 1983, 1987a, Harris 1984, Wilcox and Murphy 1985). Fragmentation is often considered to have two components: (1) decrease in some habitat type or perhaps all natural habitat in a landscape; and (2) apportionment of the remaining habitat into smaller, more isolated pieces (Wilcove *et al.* 1986). Although the latter component is fragmentation per se, it usually occurs with deforestation or other massive habitat reduction (Harris 1984). An almost inevitable consequence of

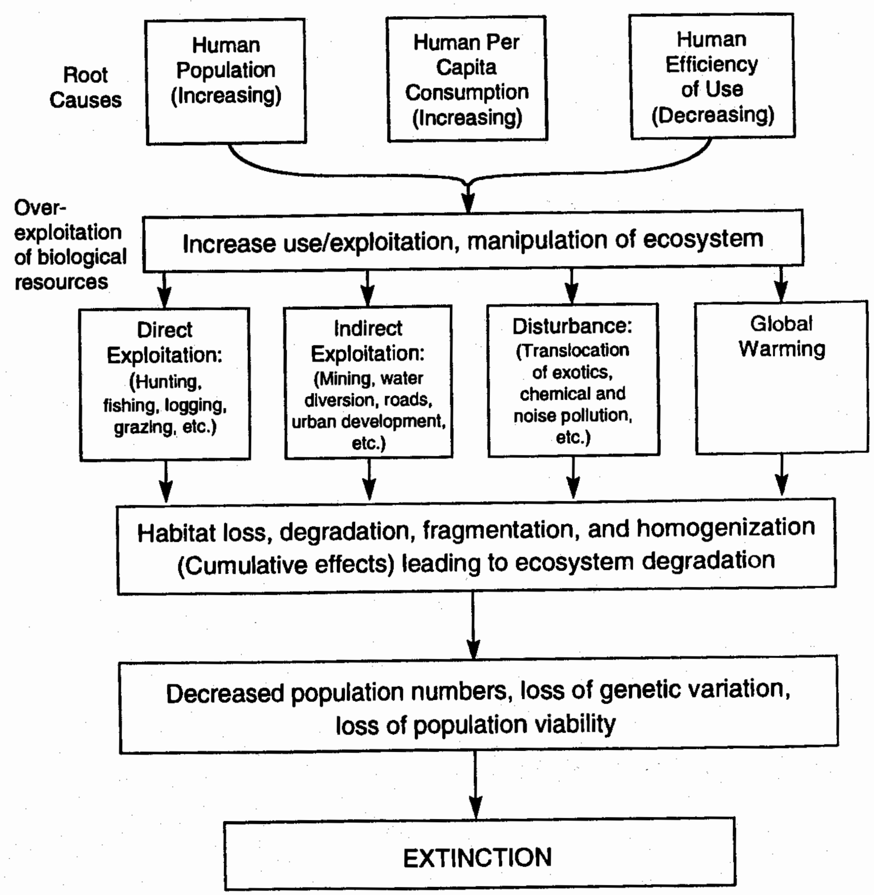

FIGURE 2.4 Relationship between root causes, overexploitation of resources, and loss of biodiversity. The final result is extinction.

human settlement and resource extraction in a landscape is a patchwork of small, isolated natural areas in a sea of altered land. A case study of fragmentation in Wisconsin (Fig. 2.5) shows a gradual reduction in forest area, accompanied by trends toward smaller and more isolated patches, as a forested landscape was converted to agriculture.

As usually happens in science, as ecologists learned more about fragmentation, the process turned out to be much more complex than once thought. Early fragmentation studies viewed the process as a species–area problem analogous to the formation of land-bridge islands as sea levels rose since the Pleistocene. Hence, island biogeographic theory was invoked to explain losses of species as the area of habitats declined and their isolation increased. Certainly, there are good analogies between real islands and caves, lakes, prairies in a forested landscape, or pieces of remnant forest in agricultural land. But there are differences, too. The water that surrounds real islands provides habitat for few terrestrial species. In contrast, the matrix surrounding habitat islands may be a rich source of colonists to the island, many of which are invasive weeds or predators on species inhabiting the island. Thus, species richness does not always decline on isolated habitat patches, as predicted by island biogeographic theory. Richness may even increase (at least temporarily) as species invade from adjacent disturbed areas. In such a case, species composition often shifts toward weedy, opportunistic species while sensitive species of habitat interiors are lost (Noss 1983, Lynch 1987). The matrix in a fragmented landscape is also in a state of flux, as crops are planted and harvested, as tree plantations go through their rotations, as farming or silvicultural methods change, and as human settlements grow and decline. Thus the external environment of a habitat patch is not as constant or predictable as the water surrounding a real island.

Fragmentation is a process and ecological effects will change as the process unfolds (Fig. 2.6). In the early stages of the process, the original landscape is perforated by human-created openings of various sizes, but the matrix remains natural habitat. At this stage, we would expect the abundance of native species of the original landscape to be affected little, although the access created by human trails or roads may reduce or extirpate large carnivores, furbearers, and other species subject to human exploitation or persecution. Such losses are well documented historically. Also, a narrow endemic species whose sole habitat just happened to be in an area converted to human land use would also be lost. As human activity increases in the landscape, the gaps in the original matrix become larger, more numerous, or both, until eventually they occupy more than half of the landscape and therefore become the matrix. A highly fragmented landscape may consist of a few remnant patches of natural habitat in a sea of converted land. Many landscapes around the world have followed this pattern of change.

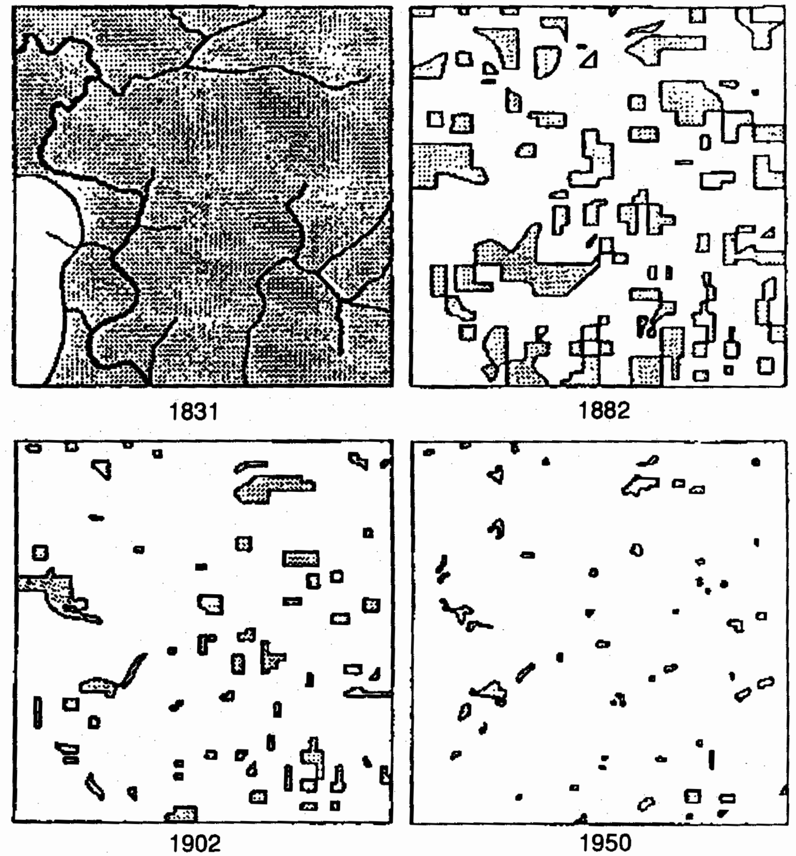

FIGURE 2.5 Changes in wooded area of Cadiz Township, Green County, Wisconsin, during the period of European settlement. Shaded area represents the amount of land in forest in 1831, 1882, 1902, and 1950. From Curtis (1956). Used with permission of the University of Chicago Press.

Fragmentation does not necessarily spell extinction. A species might persist in a highly fragmented landscape in three ways. First, it might be able to survive or even thrive in the matrix of human land use. A number of weedy plants, insects, fungi, microbes, and vertebrates such as European starlings and house mice fit this description. Second, it might be able to maintain viable populations within individual habitat fragments; this is an option only for plants, microbes, and small-bodied animals with modest area requirements. Or third, it might be highly mobile. A mobile species could integrate a number of habitat patches, either into individual home ranges or into an interbreeding population. Pileated woodpeckers, for example, have learned to fly among a number of small woodlots to forage in landscapes that were formerly continuous forest (Whitcomb et *al.* 1981,

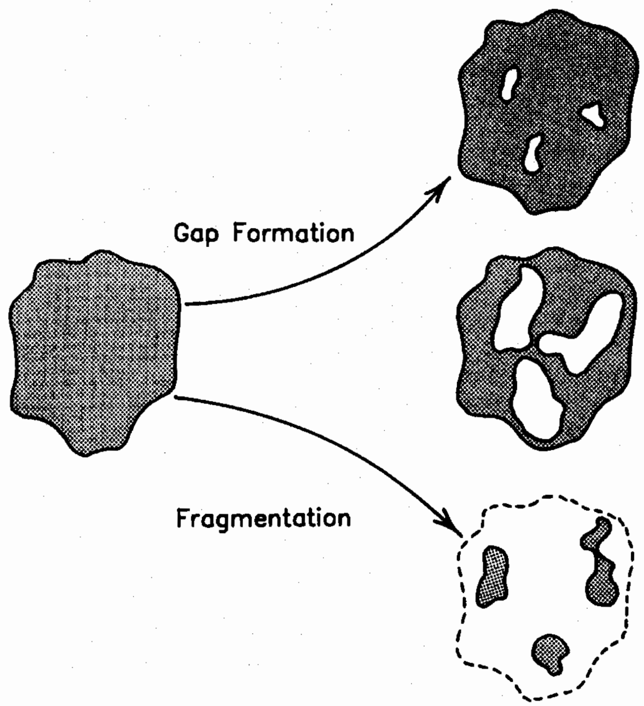

FIGURE 2.6 A fragmentation sequence begins with gap formation or perforation of the landscape. Gaps become bigger or more numerous until the landscape matrix shifts from natural to anthropogenic habitat. From Wiens (1989). Used with permission of the author and Cambridge University Press.

Merriam 1991). A species incapable of pursuing one or more of these three options is bound for eventual extinction in a fragmented landscape.

Besides the problem of small populations in small habitat patches being more likely to go extinct, small patches are also greatly affected by their surroundings. Sun, wind, rain, and other physical factors create an environment near the edges of a habitat patch different from that in the interior, particularly for forests with relatively closed canopies. Predators, competitors, and parasites may also thrive in the disturbed habitat near an edge and penetrate some distance into the patch.

Roads. Roads are increasingly being recognized as a severe threat to sensitive wildlife and natural ecosystems. Wilderness advocates have long fought road-building proposals, largely on recreational or scenic grounds. However, biology also provides evidence of detrimental effects of roads. Landscape ecologists have found that roads block movement of small animals.

Wildlife biologists recognize problems with open roads that expose large mammals to heavy hunting pressure, poaching, and harassment. Fisheries biologists worry about sedimentation of streams as a result of slope failures and erosion from roads. Humane societies worry about roadkills. And conservationists are concerned about the role of roads in stimulating more development and resulting habitat destruction. Only recently have biologists recognized that the cumulative effect of all these factors constitutes a leading threat to biodiversity.

Roads are movement barriers to some species of small vertebrates and invertebrates. To the extent that animals hesitate to cross roads, roads fragment populations into smaller demographic units that are more vulnerable to extinction from any number of causes. A study in southeastern Ontario and Quebec found that several species of small mammals rarely ventured onto road surfaces when the road clearance (distance between road margins) exceeded 20 m (Oxley *et al.* 1974). The mammals whose movements were inhibited by roads included eastern chipmunks, gray squirrels, and white-footed mice. In Germany, several species of carabid beetles and two species of forest rodents where shown to rarely or never cross two-lane roads. Even a narrow, unpaved forest road closed to public traffic served as a barrier (Mader 1984). In an Oregon study, dusky-footed woodrats and red-backed voles were found at all distances from an interstate highway but never in the highway right-of-way, suggesting that these rodents did not cross the highway (Adams and Geis 1983). Road clearances can also be barriers in more open habitats. In a study of the effects of a highway on rodents in the Mojave Desert (Garland and Bradley 1984), only one white-tailed antelope squirrel, out of 612 individuals of eight species captured and 387 individuals recaptured, was recorded as having crossed the road. A nine-year study in a Kansas grassland found that very few prairie voles and cotton rats ever crossed a dirt track 3 m wide that bisected a trapping grid (Swihart and Slade 1984). Many other studies have documented barrier effects of roads (Bennett 1991), even for animals as large as black bears (Brody and Pelton 1989).

Paved roads often affect mortality rates more directly; more than one million vertebrates are killed each day on roads in the United States (Lalo 1987). In Florida, roadkill is the leading known cause of death for all large and medium-sized mammals, with the single exception of the white-tailed deer (Harris and Gallagher 1989). Roads through national forests, such as the Ocala National Forest in Florida, are significant mortality sites for threatened vertebrates. In the Big Cypress National Preserve, expensive underpasses and fencing have been constructed to channel movement of Florida panthers under Interstate 75. Panthers and other animals have used these underpasses, but holes in the highway fenceline limit their effectiveness and point to a need for frequent maintenance (Foster and Humphrey 1991).

Another impact of roads stems from the access they provide to legal and illegal hunters. Open road density has been found to be a good predictor of habitat suitability for large mammals, with habitat "effectiveness" and population viability declining as road density increases. The sensitivity of hunted elk populations to open road density is well established. According to research in the Northwest and the northern Rockies, a road density of one mile per square mile of habitat can decrease habitat effectiveness for elk by 40 percent, compared to roadless watersheds. As road density increases to six miles per square mile, elk habitat use falls to zero (Lyon 1983, Wisdom *et al.* 1986). Mountain lions may also avoid roads. In Arizona and Utah, existing populations of cougar are concentrated mostly in areas of low road density, but road avoidance was found to be limited to paved and improved dirt roads (Van Dyke *et al.* 1986).

Studies in northern Wisconsin and Minnesota have found that wolves cannot maintain populations where road density exceeds about 0.9 miles per square mile (Thiel 1985, Mech *et al.* 1988). Wolves generally do not avoid roads and often follow them as convenient travelways. But following roads brings them into contact with people who shoot them. Similarly, most grizzly bears die near roads, and, in many areas, grizzly habitat use near roads is significantly reduced (McLellan and Mace 1985, McLellan and Shackleton 1988). Mattson *et al.* (1987) found that grizzlies in Yellowstone National Park are also harmed by roads. Adult females and subadult males displaced by dominant bears into areas near roads and developments have a greater chance of being killed. Mattson and Knight (1991) concluded that, given uncertainty about the viability of the Yellowstone grizzly population, "we cannot afford to increase the area impacted by secondary roads and major developments."

Black bears can also be vulnerable to road access and may not be able to maintain populations in the southern Appalachians where road density exceeds 0.8 miles per square mile (Brody 1984). The vulnerability of black bears to road access in the Appalachians results from unusually high poaching pressure. In the Great Dismal Swamp of Virginia and North Carolina, roads may not be such a threat. A protected bear population spent more time near roads than expected and used roads as travel corridors (Hellgren *et al.* 1991). In much of the West, black bear populations persist in areas with fairly high road densities, perhaps because poaching is not yet intense. This persistence could be temporary, however. With increased value of bear gall bladders and other body parts in the Asian marketplace, survival of black bears in any roaded landscape cannot be assured.

Although inhibiting dispersal of some species by blocking movement, roads also help disperse species that thrive in disturbed roadside habitats or travel by way of vehicles. In the Northwest, Port Orford cedar root rot fungus, black-stain root disease fungus, spotted knapweed, and the gypsy moth are all known to disperse and invade natural habitats via roads and vehicles (Schowalter 1988). Other deleterious effects of roads, too numerous to elaborate here, include soil and water pollution, erosion, sedimentation of streams and decline of fisheries, edge effects, overcollecting of rare plants and animals (for example, cacti and king snakes), elimination of snags (upon which many cavity-nesting birds and mammals depend) for firewood or road safety, and a number of indirect and cumulative effects (Diamondback 1990, Bennett 1991).

Many land managers close roads to public use at least seasonally to protect wildlife such as elk or grizzly bears. However, the barriers erected may be inadequate, and many driveable roads are not included in agency road inventories. A detailed study on the Flathead National Forest in Montana found that the Forest Service failed to include in its inventory 70 percent of the short-term and temporary roads. Some 80 percent of "obliterated" roads inventoried by the Forest Service were driveable by ordinary passenger vehicles, and 38 percent of the barriers erected for road closures were ineffective (Hammer 1986, 1988, 1990). A study by the Oregon Department of Fish and Wildlife found that roads planned for closure after timber sales on the Siuslaw National Forest were actually closed only 21.4 percent of the time (Ingram 1991). Even roads truly closed to public use, unless fully revegetated, still function as movement barriers to small animals, as sources of sediment to streams, and as trails along which poachers may walk.

Thus, road construction, road use, and the physical road itself may have a number of negative effects. A decision to build a new road or upgrade an existing road must be considered carefully. The need for a critical assessment of potential road impacts is especially strong where habitat of threatened or endangered species is involved. In many such cases, not only is it desirable to prevent new roads from being built; it may also be advisable to close and obliterate existing roads.

Global warming. A looming threat to biodiversity is global warming (Peters and Lovejoy 1992). The predicted warming is a result of increasing levels of carbon compounds in the atmosphere, especially carbon dioxide (CO_2) but also methane and others. Atmospheric CO_2 comes from a variety of sources, the primary ones being combustion of fossil fuels (oil and coal) and the cutting and burning of forests worldwide. This increase in CO_2 creates a "greenhouse effect" that warms the earth's surface. Current estimates are that atmospheric CO_2 is increasing at a rate of 1 to 2 percent per year, resulting in a doubling of atmospheric CO_2 in about 50 years, with resulting temperature rises of from 1 to 5°C.

A warming of 3°C (the median prediction) would result in a world warmer than it has been for the past 100,000 years and would cause massive changes in species distributions and ecological processes. Sea levels would rise, patterns of rainfall would change, and storms and wildfires would increase in many regions. An increased temperature of 3° is equivalent to a latitudinal shift of about 250 km (156 miles) or an altitudinal shift of 500 m (0.3 miles). Species already confined to the tops of mountains could be extirpated as their habitats are "pinched off" (Fig. 2.7). Other species could presumably move north, although the rate of change expected may be 10–40 times more rapid than previous changes in climate, at least since the Pleistocene, making it difficult for species to migrate quickly enough. Further-

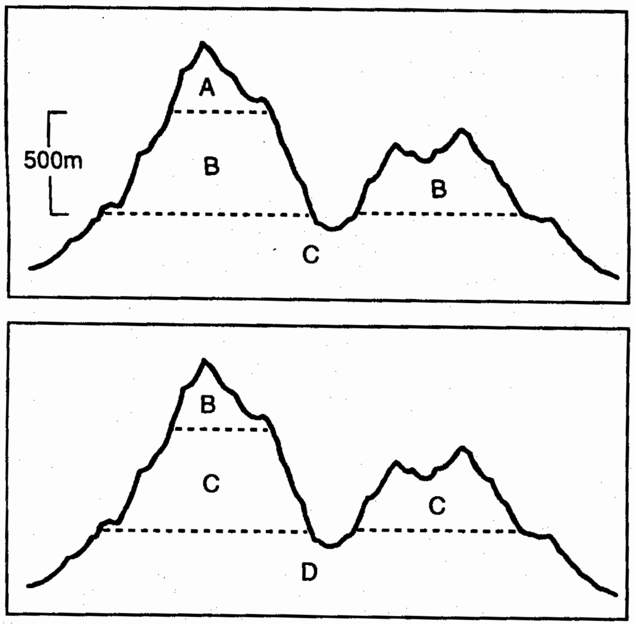

FIGURE 2.7 Response of species to global warming by shifting altitudinal distribution. (*Top*) Initial altitudinal distribution of three species, A, B, and C. (*Bottom*) Species distribution after a 500-m shift in altitude in response to a 3°C rise in temperature. Species A becomes locally extinct. Species B shifts upward, and the total area it occupies decreases. Species C becomes fragmented and restricted to a smaller area, while species D successfully colonizes the lowest altitude habitats (from Peters 1988).

more, changes in climate would be taking place concurrently with habitat fragmentation and other human stresses on biodiversity, resulting in many cumulative impacts (Fig. 2.8).

CONSEQUENCES

As the intermediate impacts on ecosystems intensify and accumulate, populations of many species decline. Decline is usually accompanied by loss of genetic variation, uneven sex ratios, and other threats to the viability of

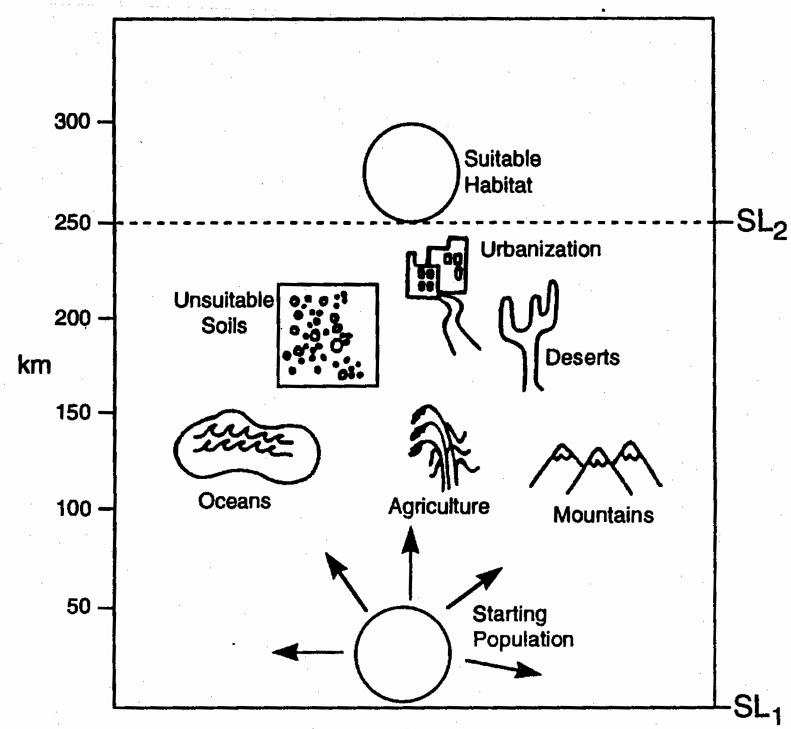

FIGURE 2.8 Response of species to global warming by shifting latitudinal distribution. The figure illustrates a plant species consisting of a single population with a distribution determined solely by temperature. After a 3°C rise in temperature the population must shift 250 km to the north (from SL_1 to SL_2) to survive. Shifting might occur by simultaneous range contraction from the south and expansion by dispersal and colonization to the north, which depends on propagules being able to find suitable habitat to mature and in turn produce propagules that can colonize more habitat to the north. Propagules must pass through or around natural and artificial obstacles like mountains, lakes, cities, and farm fields (from Peters 1988).

populations. These proximate factors are what directly lead populations down a virtually inescapable vortex to extinction (Gilpin and Soulé 1986).

The most basic rule about population viability is that small populations are more vulnerable to extinction than larger populations. Analyses of population viability attempt to determine the probability that a particular population will persist for a given period of time, and ask something like: "What is the size of the population that has a 95 percent chance of surviving 100 years?" With few exceptions, populations on the order of thousands of individuals appear necessary for long-term persistence (Soulé 1987, Thomas 1990). Population viability analysis also allows one to ask questions about the probability of persistence under different management scenarios. For example, how much will the probability of persistence increase for a population of grizzly bears if we reduce mortality rates by reducing road density from 3 miles to less than 0.5 miles per square mile?

Several factors, both random and deterministic, predispose small populations to extinction (Shaffer 1981, Soulé 1987). The most important of these factors are reviewed below.

Environmental variation and natural catastrophes. Bad winters, droughts, hurricanes, and other random or unpredictable environmental phenomena affect both large and small populations. As a result, all populations fluctuate through time. Small populations are simply more likely to fluctuate down to zero. A species with a large geographical range has less chance of all of its members experiencing the same environmental variation, especially for catastrophic events such as hurricanes, but also for less pronounced changes in habitat conditions. In a given year, some parts of the range may have favorable weather and other parts experience drought. A species with a restricted range has no such spatial buffer.

When a population of one species fluctuates, populations of other species with which it interacts may also fluctuate. A poor mast year for oaks is a bad year for acorn-eating mammals and birds. A rare species can be especially vulnerable to population increases among its predators, competitors, parasites, and diseases (Shaffer 1981). If an exotic predator invades a small habitat island, it can quickly extirpate suitable prey species. Introduced rats, cats, and other predators have been a primary source of extinctions on oceanic islands (Vitousek 1988).

Predictable environmental change can also threaten small populations, especially in fragmented landscapes. Natural succession may eliminate meadows and other early seral habitats upon which certain species depend. As trees invade, sun-loving wildflowers and butterflies may perish. In small islands, the chances of natural disturbances occurring and creating earlier

successional habitats are reduced (Pickett and Thompson 1978, Gilbert 1980).

Demographic stochasticity. Chance variation in age and sex ratios and other population parameters, termed *demographic stochasticity*, can change birth and death rates. In small populations, extinction occurs quickly when deaths outpace births (Lande 1988). Some species have a threshold density or number of individuals below which the population cannot recover. This *Allee effect*, named after the animal ecologist W.C. Allee, is likely when organisms modify their environment physically or chemically to encourage their survival, when group defense against predators is necessary, or when social interactions and mating success depend upon some critical population density. In the United States, extreme sociality may have contributed to the extinctions of the Carolina parakeet, passenger pigeon, and heath hen (Soulé 1983). The decline of these populations to some threshold level may have stifled reproductive behavior and led to rapid extinction.

Genetic deterioration. If we consider the fate of populations over a fairly long time span, genetic integrity becomes virtually as important as demographic stability to persistence. Small, isolated populations on habitat islands are prone to two kinds of genetic problems: inbreeding depression (caused by mating between close relatives) and genetic drift (a random change in gene frequencies). Populations with low genetic diversity may show reduced fertility and survivorship, especially when inbred, and in the long run will be less able to respond adaptively to environmental change (Frankel and Soulé 1981, Schonewald-Cox *et al.* 1983). The Florida panther, for example, has been restricted to south Florida for many decades due to habitat destruction and persecution across the rest of its original range in the Southeast. The remaining population of fewer than 50 individuals is suffering effects of inbreeding, including reduced fertility (Ballou *et al.* 1989). Ultimately, small populations on habitat islands, if they survive at all, may lose their evolutionary potential unless enriched by gene flow from other populations.

Metapopulation dynamics. Many species are apparently distributed as metapopulations, that is, as systems of local populations linked by occasional dispersal that wards against demographic or genetic deterioration (Levins 1970, Gilpin and Hanski 1991). Marshes and other wetlands, for example, are often distributed as patches corresponding to potholes or other topographic depressions. Species restricted to these wetlands have populations scattered about the landscape. It is the fate of these local populations to wink off and on over time. Dispersal from one wetland to another allows for recolonization of vacated habitats, or genetic enrichment of an existing population, so the metapopulation as a whole persists.

Suppose that urban development occurs in the upland matrix in which the wetlands are found. Frogs, water snakes, turtles, muskrats, and other aquatic animals that once dispersed through the forest between wetlands now face significant barriers to movement: roads, buildings, parking lots, and the like. Meanwhile, development may drain or pollute many of the wetlands. The wetlands may be visited by children who like to collect small animals for pets. When a local population is extirpated in this scenario, it has little chance for reestablishment. If local populations go extinct but are not reestablished, the entire metapopulation (and eventually, perhaps, the species) gradually dies off. Because increases in local extinction rates and declines in immigration rates are cumulative effects, even common species are not immune to the effects of widespread habitat alteration and fragmentation.

Current Status of Biodiversity in North America

Although most people now realize that biodiversity is declining, no comprehensive statistics are available to document all aspects of this loss. People have simply not been keeping good track of their natural heritage. Nevertheless, ample evidence suggests that substantial impoverishment has occurred in North America and that the rate of loss is increasing. Some general aspects of this impoverishment were reviewed in Chapter 1. Here, we present additional information.

Species Loss

At least 71 vertebrate species and subspecies have gone extinct in North America, north of Mexico, over the last 500 years (Nature Conservancy 1992), plus perhaps 217 full species of plants (Russell and Morse 1992). Undoubtedly many more invertebrates, nonvascular plants, fungi, and bacteria have been lost, with most of these extinctions going unnoticed because many of the species were not even known to science. The United States has never had a systematic biological inventory, so the total number of extinctions can only be guessed.

One obvious indicator of biotic impoverishment is the number of species listed under the Endangered Species Act (Table 2.2). In the United States alone, some 796 species were listed as threatened or endangered as of May 1993, and thousands more are candidates for listing. As noted in Chapter 1, very few species listed under the Endangered Species Act have shown any evidence of recovery. More alarming, the implementation of the Act by federal agencies virtually precludes recovery. An analysis of U.S. Fish and Wildlife Service recovery plans found that 28 percent of recovery goals were set at or below the size of the species population at the time the recovery plans were written; 60 percent of vertebrates had recovery goals that would keep them biologically endangered (Tear *et al.* 1993).

Furthermore, many species such as bison have been extirpated from most of their original range in North America but are not listed as endangered or threatened because the remaining populations appear stable. Many more species have been gradually fragmented into small populations that may be slowly on their way to ultimate collapse. Indeed, population viability theory (as reviewed above) suggests that the present diversity of species in landscapes across the continent is temporary. Indeed, we may be seeing the "living dead."

Ecosystem Degradation

Species extinction is only the last and most obvious stage of biotic impoverishment. Of greater long-term concern is the degradation of ecosystems and landscapes. Measures of ecosystem loss or dysfunction are not as straightforward as species extinctions, in part because ecosystems are much less easy to classify. No accepted national classification of vegetation exists for the United States. Nevertheless, statistics on broad landscape categories such as deserts, wetlands, riparian areas, forests, and rangelands (and on more specific associations in many regions) suggest that habitat loss and degradation are widespread in North America (Noss *et al.* 1994).

Loss of forests in the United States after European settlement proceeded as rapidly as in any region of the world. By 1920, some 96 percent of the virgin forests of the northeastern and central states had been logged, with other regions not far behind (Reynolds and Pierson 1923). By 1980, some 85 percent of the virgin forests in the United States had been destroyed, with losses estimated as 95 to 98 percent for the conterminous 48 states (Postel and Ryan 1991). Some forest types today remain in only a fraction of their former abundance. Old-growth forests of the Pacific Northwest are a well-known example, with losses approaching 90 percent (Norse 1990). Longleaf pine, which once dominated the uplands of the southeastern coastal plain, has been reduced by over 98 percent since settlement and is our most endangered major forest type (Noss 1989). Not all of the loss of longleaf pine can be blamed on logging; some is due to fire suppression, which results in invasion of stands by hardwoods and loss of native species dependent on

TABLE 2.2 Number of Species Listed as Endangered or Threatened in the United States as of November 30, 1992[a]

Category	Endangered	Threatened	Total
Mammals	56	9	65
Birds	73	13	86
Reptiles	16	18	34
Amphibians	6	5	11
Fishes	55	36	91
Snails	7	6	13
Clams	40	2	42
Crustaceans	9	2	11
Insects	14	9	23
Arachnids	3	0	3
Plants	298	72	370
TOTAL	577	172	749

[a] From USDI, Fish and Wildlife Service 1992.

open, sunny conditions. Many other forest types in the United States can be considered endangered or threatened (Noss *et al.* 1994).

Rangelands in the United States have been described as deteriorated in a series of reports beginning in 1936 (U.S. Department of Agriculture 1936; USDI Bureau of Land Management 1962, 1975a, 1975b; U.S. Comptroller General 1977; U.S. General Accounting Office 1988a, 1988b, 1991; Wald and Albersworth 1985, 1989). The Bureau of Land Management has recently claimed that public rangelands are in improved condition (U.S. Bureau of Land Management 1990), but has presented no credible evidence to support this contention. In fact, their own estimates suggest that at least 52 percent of the public ranges are in lower seral stages [mid-seral = fair (36 percent); early seral = poor (16 percent)]. One could argue that a certain proportion of rangelands would be in this category naturally, but the percentages would be quite different and seral stages would shift across the landscape over time (see Chapter 7). Very few areas in the West have not been grazed at some time by livestock. For sagebrush steppe, a major vegetation type in the Intermountain West, less than 1 percent has never been grazed and 30 percent has been heavily grazed, with dominance concentrated in a few woody plants (West 1994).

Grasslands and savannas are generally the most endangered terrestrial ecosystems in the United States, with most losses due to conversion to agriculture and, secondarily, to fire suppression or overgrazing and subsequent invasion by exotics. Among the types that have declined in extent by over 98 percent since European settlement are longleaf pine savannas and *Arundinaria gigantea* canebrakes in the Southeastern Coastal Plain; tallgrass prairies east of the Missouri River and on mesic sites everywhere; bluegrass savanna–woodland and prairies in Kentucky; Black Belt prairies in Alabama and Mississippi and Jackson Prairie in Mississippi; oak savanna in the Midwest; wet and mesic coastal prairies in Louisiana; lakeplain wet prairie in Michigan; sedge meadows in Wisconsin; Hempstead Plains grasslands on Long Island (New York); prairies and oak savannas in the Willamette Valley of Oregon; the Palouse Prairie of Oregon, Washington, and Idaho, plus similar communities in Montana; and native grasslands of all types in California (Noss *et al.* 1994).

The degradation of wetlands is similarly severe and is better documented than most ecosystem declines because of the long-standing interest of hunters and conservationists in wetlands. Nationally, 50 percent of animals and 33 percent of plant species listed under the Endangered Species Act (as of 1989) are dependent on wetlands (Nelson 1989). Yet because of draining and filling, many wetlands have been totally converted to nonwetland habitats such as agricultural fields and home sites. Estimates are that only 45 percent of original wetlands and 10 to 30 percent of original riparian vegetation remain in the United States. In some regions, the losses have been much greater, with many midwestern states and the Central Valley of California having less than 10 percent of their original wetlands (Dahl 1990, Noss *et al.* 1994). Some 98.5 percent of the riparian vegetation of the Sacramento River in California has been destroyed (U.S. Congress, Office of Technology Assessment 1967).

Finally, statistics about water are equally alarming. Water quality and availability have deteriorated in virtually every region of the United States. Only 3.9 percent of the nation's streams are considered to have "maximum ability to support populations of sport fish and species of special concern" (Judy *et al.* 1984) and less than 2 percent of streams in the 48 conterminous states are of high enough quality to be worthy of federal designation as wild or scenic rivers (Benke 1990). Astoundingly, almost all of the water in the Colorado River is diverted before it reaches the Gulf of California (*High Country News* 1987). We can be sure that the "water wars" of the West will intensify if current population and consumption trends continue, and that aquatic habitats nationwide will be increasingly endangered (see Chapter 8).

Conclusion

Human civilization, particularly the European variety, has not been kind to North America. The geological, physical, ecological, and biological forces that naturally generate biodiversity have not ceased operating; they will go on long after human civilization as we know it has crumbled. But natural forces have been overwhelmed over the last few centuries by the plow, bulldozer, chainsaw, dredge, dam, and other tools and artifacts of civilization, and by simply too many people consuming too much of everything. Biodiversity at every level is critically imperiled. Can we "wise up" and begin turning degenerative trends around? The following chapters will consider this question in some depth.