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Threats to Biological Diversity In The United States

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THREATS TO BIOLOGICAL DIVERSITY IN THE UNITED STATES

I SUMMARY

As worldwide threats to biodiversity increase and extinction rates rise to 1000 times the natural background extinction rate, the conservation of biological diversity is emerging as a major public policy issue. The ever-expanding human population, the increasing per capita consumption of goods, and the greater impacts of pollution on local, regional, and global scales have increasingly stressed the living systems which provide humans with food, raw materials, medicines, breathable air, drinkable water, current climatic patterns and aesthetic pleasure.

Building on realizations over the last two-decades that technological advancements are degrading a potentially fragile natural world and that whole ecosystems are endangered, the biodiversity movement surfaced in 1979-80 with the publication of several landmark documents, including <u>The Sinking Ark</u> by Norman Myers, Thomas Lovejoy's extinction section of <u>The Global 2000 Report to the President</u>, and <u>Conservation Biology--an Evolutionary-Ecological Perspective</u> by Soule and Wilcox.

Biological diversity refers to the variety of life on all levels of organization, represented by the number and relative frequencies of items (genes, organisms and ecosystems). Perhaps the most useful definition involves these three levels: 1) **genetic diversity** within species; 2) **species diversity**, or the numbers and frequencies of species; and 3) **ecosystem diversity**, the variety of communities of organisms in their physical settings. Unlike wildlife management or endangered species protection, practices which strive to protect only certain favored species, conservation of biological diversity recognizes species, genotypes and functioning ecosystems as valuable resources and recognizes communities of organisms as interactive complexes to be preserved.

In a policy sense, the concept of biological diversity represents a potential measuring tool for the preservation of biological integrity. Measurement of biological diversity could provide an effective and economical indicator of overall ecological health and help ensure that adequate protection of ecosystems is achieved.

Before discussing anthropogenic threats to biodiversity, it is useful first to examine how genotypes, species and ecosystems **respond to anthropogenic stress** in general, and to examine what factors determine vulnerability to anthropogenic stress. Human activities reduce **genetic diversity** by eliminating whole populations of organisms, by reducing populations to the point where genetic drift overtakes natural selection as a dominant evolutionary force, and by creating new selection pressures. **Species** exposed to irresistible anthropogenic stress may become increasingly rare, locally extinct, and eventually extinct throughout their range. **Ecosystems** tend to employ self-regulating mechanisms that enable them to withstand some natural stresses with little or no effect, and to recover from some stronger stresses which do have an effect, but anthropogenic stresses are often drastic and quick enough to overwhelm this self-regulation.

Many factors determine **vulnerability of species**. Some are inherent properties of the organism or species and impart vulnerability whether the stressor be natural or anthropogenic; others result largely from the nature of anthropogenic stressors. Many of these factors are correlated, but can exist independently (e.g. many species of large organisms have small populations, but both factors, large organism size and small population size, can independently cause vulnerability).

Species with **small effective population size** (referring to the number of breeding males and females) are vulnerable for demographic (e.g. unbalanced sex ratios) and genetic reasons (e.g. limited gene pool, subject to genetic drift). This may be the primary risk factor, especially in recently reduced populations. Species with a **narrow geographic distribution**, those with **large area requirements**, and those **"amphibious"** species requiring more than one type of habitat are at increased risk that some stressor will infringe on at least one of their habitats.

Specialists, requiring a particular type of habitat or food, and species **intolerant** of disturbance are at greater risk due to their inflexibility. Species of **large organism size** are vulnerable despite the advantages of large size because many natural and anthropogenic stressors (e.g. hunting) select against large organisms. Organisms with **slow reproductive rates** are more vulnerable to increases in mortality. **Evolutionarily naive** organisms that have evolved in the absence of competitors, predators and diseases are more vulnerable to the accidental or intentional introduction of such organisms.

While factors imparting vulnerability to species are the most well-known, factors increasing vulnerability to sub-specific populations and genotypes, and to ecosystems, must also be addressed. Each factor listed above may also affect **sub-specific populations.** Broad principles concerning **genetic determinants** of vulnerability are not well defined, but genes conferring the ability to reproduce early would increase fitness in populations heavily exploited by humans.

Six factors are primarily involved in imparting **vulnerability among ecosystems. Impermanent** ecosystems, particularly those that are actually successional stages, are vulnerable to human activities which intentionally or unintentionally prevent natural disturbance or succession (e.g. fire suppression). **Oligotrophic** ecosystems (those in which nutrient elements are scarce and limiting to many organisms) are vulnerable to changes in nutrient availability (e.g. increases from fertilizer use, sewage discharge). **Undersaturated** ecosystems, exhibiting fewer species than might be expected due to current isolation or historical reasons, may contain vacant niches and naive biota which are vulnerable to invasion. **Isolated** ecosystems, such as islands, are vulnerable because extinction is not fully offset by outside colonization. Ecosystems of **small size** sustain fewer species than a region of similar size within a larger ecosystem due to penetration of external influences. The most important risk factor is probably **proximity to human populations.** Ecosystems suffer as human populations appropriate land and resources and produce harmful wastes.

Most current and pressing environmental problems, including the biodiversity crisis, primarily result from two trends: the **exponentially increasing human population** and the **increasing per capita consumption** of the Earth's resources to provide for human needs. These ultimate causes are manifested in **six proximate causes** representing the major anthropogenic stressors to biological diversity.

Direct population reduction occurs in the form of **intentional taking** (hunting, trapping, fishing and collecting) and **incidental taking** (capturing or killing of non-target organisms during hunting, trapping etc.). Most industrialized nations now limit direct reduction in some manner to prevent over-exploitation of resources, but over-exploitation remains a major stressor to large mammals in many developing countries (e.g. African elephants and rhinoceroses). Incidental taking is responsible for the death of great numbers of marine organisms, including marine mammals, sea birds, sea turtles and some species of fishes which are unintentionally trapped and killed in driftnets.

Once the most severe threat posed by Homo sapiens, direct reduction has been eclipsed by **physical alteration of habitat.** Physical alteration can be complete, as in the **conversion** of wildlands to agricultural or urban land, or partial, involving creation of barriers to organism dispersal (**ecosystem fragmentation**) or deletion of some ecosystem component or components (**ecosystem simplification**). The clearcut logging of sections within a forest (fragmentation), or the selective logging of standing dead trees within a forest (simplification) will both have repercussions for the ecosystem beyond the simple loss of trees. Most significantly at risk are some species of the following categories: large terrestrial mammals, bats, hole-and ground-nest birds, amphibians, snails, conifers, herbs, grasslands, freshwater stream organisms, river fishes and molluscs, and estuarine vegetation.

A number of **chemicals and waste products** produced by human beings have adverse effects on biological diversity. The biotic community structure in unbuffered lakes and streams has been heavily impacted by acid deposition, and though currently controversial, effects on coniferous and deciduous forest ecosystems may prove similarly destructive. Tropospheric ozone is believed to have severe effects on coniferous and deciduous forests. Excessive nutrients are a major hazard to unbuffered lakes and can cause major problems in estuaries and coral reef ecosystems. Pesticides can have high ecological impacts in freshwater and estuarine ecosystems, and have been implicated in bird kills. Plastic pollution has proven a very serious threat to marine mammals, birds and turtles. Organisms feeding at or near the top of the food chain are particularly at risk to toxic substances which bioaccumulate (e.g. PCBs). Not even the National Wildlife Refuges are safe from these threats, as evidenced by a recent survey of contamination in these reserves following the discovery of chemical contamination in the Kesterson Refuge.

The least understood and potentially most devastating threat to biodiversity is **global atmospheric change**, in the form of climate change and enhanced ultraviolet-B radiation. Predictions of warming and related climatic change patterns are very uncertain, but it is probable that shifting temperatures and climatic and hydrologic factors will cause species to migrate, adapt or die out. Species migration will be hindered by anthropogenic barriers such as static wildlife refuge borders, urban areas, agricultural lands, and highways. The effects of increased UV-B are even less certain, but could include disruption of marine planktonic communities, effects on tree seedlings, and DNA and immune system damage, increased skin cancers and cataracts in mammals. Additionally, higher atmospheric CO_2 levels may have direct effects on organisms.

The introduction of an **alien species** can upset ecosystem functioning due to new forces of competition, predation and disease or due to more indirect factors. While alien species usually do not survive upon introduction into a new habitat, those that do survive have the opportunity to flourish in a new habitat devoid of their natural enemies. Alien species have been most destructive to naive and undersaturated biota, such as in Hawaii. In general, terrestrial and freshwater organisms are more likely to be affected than marine species, as their populations are more localized.

As the magnitude and scope of these threats continue to increase, and as new threats continually appear, **interactions** between stressors will become more important. While currently not well studied or understood, interactions between two or more stressors could produce cumulative effects which are far more destructive than the individual threats; this interaction must be considered to ensure adequate protection.

An **overview** of the effects of 13 stressors on 59 categories of organisms in the contiguous 48 states appears in **Table 2**. The effect of each stressor on each category of organisms is rated as negligible/minor, substantial meriting study, or very serious meriting immediate attention. Table 2 represents the best estimate of the author, Elliott Norse, with consideration given to the opinion of avian ecologist David Blockstein. Table 2 could be improved at some future time by accounting for geographic differences, showing change in stressors over time, incorporating effects of interactive stressors, including the views of additional scientists, including bacteria and other unrepresented categories of organisms, and producing similar charts for the biota of Hawaii, Alaska, United States territories and other nations.

Some categories of organisms, such as birds, have been more intensively studied than others, and may provide some indications of the status of biological diversity in the United States. An **in-depth review of United States bird populations** indicates that populations of seabirds (except terns), colonial wading birds (except endangered wood storks), raptors (except harriers, some hawks, et al.), and shorebirds (except three declining species) appear to be stable or increasing, while many populations of waterfowl, songbirds and island birds are declining.

II INTRODUCTION

A CONTEXT

Roughly 3.5 billion years of evolution have left the earth host to perhaps 5 to 30 million extant species (Wilson, 1986). In many ways, these organisms and their forebears have shaped the world of today. Inheriting an atmosphere laden with carbon monoxide, carbon dioxide, methane, ammonia and cyanide, living organisms converted it to one of nitrogen and oxygen. Some of this oxygen reacted to form an atmospheric layer of ozone, which screened out ultraviolet radiation that had scourged the planetary surface.

Living things decomposed rocks into fine particles and added organic material, creating the world's soils. Vast amounts of atmospheric carbon dioxide were sequestered in oil, coal and limestone, thereby turning down the temperature of the global greenhouse. Much of the planetary surface was covered with trees, creating moderate microclimates and a diversity of spaces in which living organisms could hide from harsh conditions and one another. By creating breathable air, productive soils, a suitable climate and useful substances such as foods, fuels, raw materials and medicines, the Earth's plants, animals and microorganisms fashioned an environment in which Homo sapiens could originate and prosper.

Likewise, Homo sapiens has further transformed the earth, being uniquely adept at changing the world to suit its own needs. For most of human history, humans have been essentially powerless against predators, storms, droughts, famines and diseases. Currently, modern technology has provided many with relief from these stressors, as witnessed by the exponentially increasing human population, but recognition is rapidly increasing that modern lifestyles have great environmental costs.

The ever-expanding human population, the increasing per capita consumption of goods, and the greater impacts of pollution on local, regional and global scales have increasingly stressed living systems, eliminating many species and entire ecosystems. The human population is currently doubling every 40 years, forcing continued expansion onto more marginal lands and displacement of the natural inhabitants and perhaps causing a mass extinction of life like none that has happened on Earth in at least 65 million years.

The average background rate of extinction before human intervention was approximately 1 species per year; this figure was below the average rate of new speciation, resulting in a net increase in species throughout most of history. The current rate of extinction may be one thousand or several thousand species per year; this figure is significantly higher than the rate of new speciation, thus resulting in species depletion. Indeed, in the past the loss of a species has generally allowed for the emergence of one or more new species, resulting in a net increase. This is no longer true, as species which took tens of thousands of years to emerge are being extinguished and replaced by the proliferation of a single species (Myers, 1989).

Despite Homo sapiens apparent dominion over nature, humans remain reliant on the diversity of life for food, raw materials, medicines, breathable air, drinkable water, current climatic patterns, and aesthetic pleasure. Through over-exploitation, physical alteration, pollution and other manner of disturbing the multitude of species found on the earth, Homo sapiens is eliminating the source of its wealth and may be threatening its own long-term survival and well-being.

Admittedly, the newly emerging science of conservation biology lacks accurate and detailed data in most areas, including the functioning of ecosystems, the severity of threats, the effects of disturbances impacting organisms and ecosystems, and the social and economic costs of mitigating these threats. The speed with which species are being lost, however, necessitates immediate action based upon what is known. A failure to act now will result in major losses of biota. By protecting biological diversity, Homo sapiens will preserve the ecological integrity that is likely to be of great value to this and future generations.

B A PUBLIC POLICY ISSUE

The rapidly increasing threats to biological diversity have recently been paralleled by increasing awareness, creating a political environment with a still small but growing emphasis on conserving biological diversity. Like all political movements, this one has evolved over time. Many traditional peoples had cultural (often religious) rules that minimized harm to the living resources they exploited. From the beginning of agriculture some 10,000 years ago, people have saved the seeds of their crops for the next planting, thereby preserving favored genotypes. From medieval times until fairly recently, there have been conservation efforts focusing on species of utilitarian importance (mostly favored game, fish and timber species).

Thoughtful game managers have also realized that species of concern were dependent on their habitats, and pushed for habitat conservation. Beginning in the last century, the United States began protecting areas that had special scenic values in a national park system. Together, the efforts to conserve the habitats of favored species and lands of great beauty laid the foundation for ecosystem conservation.

Four realizations with origins more than a century old began taking hold about two decades ago, setting the stage for the current biodiversity movement. First, scientists, then conservationists, then a broader array of people, came to view the extinction of species as undesirable regardless of their utilitarian value. This idea has steadily gained acceptance since its incorporation into the Endangered Species Act of 1973.

The groundwork for the second realization began when Rachel Carson published Silent Spring in 1962, eloquently demonstrating that many technological advancements are unintentionally degrading nature. This point was driven home dramatically by the well-televised Santa Barbara oil spill in 1969. More than anything else, it was this realization that gave rise to the U.S. Environmental Protection Agency just a few years later.

The third realization dawned suddenly when U.S. Apollo astronauts sent back the first pictures of the small, seemingly fragile Earth within the vastness of space. Many people remarked that these pictures changed their consciousness about the finiteness and vulnerability of the world in which we live. The fourth realization, held largely within the scientific and government communities, was that whole ecosystems were rapidly being destroyed, including the supremely diverse tropical forests.

The ensuing biological diversity movement seems to have had five rather independent but almost simultaneous origins. In 1979, Norman Myers published The Sinking Ark, which examined the worldwide extinction of species of all taxa, not just the extinction of mammals and birds which had concerned previous writers. Included were the first estimates of global extinction rates. In 1980, the Council on Environmental Quality and the State Department collaborated on The Global 2000 Report to the President, which contained a groundbreaking section by Thomas Lovejoy on global species extinctions as a consequence of tropical deforestation.

That same year, the Council on Environmental Quality's Eleventh Annual Report contained a section entitled "Ecology and Living Resources--Biological Diversity" by Elliott Norse and Roger McManus (also published separately as Biological Diversity). In 1981, Paul and Anne Ehrlich published Extinction--the Causes and Consequences of the Disappearance of Species, a clarion call for conservation that reached a wider general audience. At the same time these assessments were being presented to the general public and government decision-makers, Michael Soule and Bruce Wilcox (1980) were editing and publishing a landmark volume, Conservation Biology--An Evolutionary-Ecological Perspective, a volume of scientific studies directly relevant to the extinction crisis, which gave the name to the newly coalesced science of conserving biological diversity.

C DEFINITION

The meaning of biological diversity has caused much confusion since 1980. Part of the reason stems from the newness of the concept, part from the circumstances of its origin.

The foundation for the idea of biological diversity in a conservation context began to form in the late 1950s, when ecologists such as George Evelyn Hutchinson and Robert MacArthur began thinking seriously about the related concepts of species richness and species diversity within ecological communities. In the 1970s, The Nature Conservancy used the term "natural diversity," and others used "germ plasm", "genetic resources" or "genetic diversity" to refer to the wealth of species. In 1980, Thomas Lovejoy used "biological diversity" (without definition) in Global 2000. The Council on Environmental Quality's 1980 Annual Report offered a two part definition of biological diversity, including the concepts of genetic diversity (within a species) and species richness (the number of species).

None of these adequately described biological diversity, yet the concept was useful enough to take hold. Within a year it was the focus of the State Department/Agency for International Development "Strategy Conference on Biological Diversity." Biological diversity became the explicit goal of legislation for the first time in 1983, when the U.S. Congress passed the International Environmental Protection Act. This act required United States federal agencies to help conserve biological diversity in developing countries.

The definition of biological diversity was clarified by Norse et al. (1986) and the Office of Technology Assessment (1987). Biological diversity is the variety of life on all levels of organization, represented by the number and relative frequencies of items (genes, organisms and ecosystems). Perhaps the most useful definition involves these three levels: 1) genetic diversity within species, both among individuals within a population and among different populations; 2) species diversity, or the numbers and frequencies of species within a region, and 3) ecosystem diversity, the variety of communities of organisms in their physical settings. This three-part definition now seems to be widely accepted (e.g., Reid and Miller, 1989), and is being further improved by knowledgeable scientists.

At first, this concept created confusion. Biological diversity was misconstrued as a synonym for wildlife management or endangered species. Wildlife management, as traditionally practiced, is concerned mainly with maximizing populations of beneficial animals (typically those prized for hunting) and eliminating "pests" (usually competitors). Whether by law, allocation of resources, or tradition, wildlife management was not concerned with nongame animals, plants, microorganisms, communities of organisms, gene frequencies, or evolutionary potential within species. Biological diversity is concerned with these additional factors.

Similarly, biological diversity conservation is not synonymous with endangered species protection. Recognizing that species are valuable as resources and that the biota function in important ways (such as providing ecosystem services), it is not enough to conserve only those species that are approaching the brink of extinction. Rather, conserving biological diversity is conserving the integrity of all populations, species and ecosystems, whether rare or abundant.

Loss of biological diversity is perhaps most often linked to deforestation, one of the many human actions which can reduce populations of some species (often climax species or specialists) while potentially increasing populations of others (usually lower successional species or opportunistic species). For example, current logging practices in many areas of the world, including the United States, often reduce populations of species dependant on the ancient forest habitat being destroyed (e.g. the spotted owl), but may increase populations of lower successional species or opportunistic species which take advantage of disturbance.

This has sometimes been termed "ecosystem conversion" rather than "degradation", as one value or use (wildlands providing ecosystem services and wildlife habitat) has been exchanged for another (the harvest of timber or use of land for agriculture), while degradation is reserved for the reduction in quality or productivity. While this is a valid distinction, it must be recognized that degradation is often a component of conversion; the removal of natural vegetation during conversion degrades the ability of the ecosystem to provide ecosystem services which can be vital to the maintenance of any life.

Furthermore, the replacement of climax or specialist species by lower successional or opportunist species should not be misconstrued (as it sometimes has) as an increase in biodiversity. As David Wilcove (1989) notes, while disturbance of ancient Pacific Northwest forest might attract enough lower successional and opportunistic species to increase species richness on a particular tract, this is not an increase in biodiversity. The amount of logging in this area has left no shortage of habitat for open-country species such as dark-eyed juncos and brown-headed cowbirds, whereas the species associated with old-growth coniferous forests are diminishing.

Clearly, biological diversity is not just a numbers game, and there is more to preserving biological diversity than conserving only the areas richest in species. Rather, maintaining biological diversity means maintaining the integrity of the genetic structure within populations, the richness of species within ecosystems and the mix of ecosystems that prevailed before human impact in all regions of the Earth's surface. This goal is implicit in any sound definition of biological diversity.

In a policy sense, the concept of biological diversity represents a potential measuring tool for the preservation of biological integrity. Ecologists commonly assess the severity of pollution stress on community structure by measuring either reductions in overall species diversity (species-level biodiversity) or changes in the abundance of indicator species. Indicator species fall into two categories: "decreasers" (those sensitive to the pollution stress) and "increasers" (those tolerant of the stressful conditions which expand into niches vacated by decreasers).

D PATTERNS BEFORE HUMAN IMPACT

Since very few of the world's ecosystems were studied before they underwent substantial alteration by humans, the assembling of a global picture of the pre-impact world's biota is largely an exercise in combining information from paleoecology and early written accounts with inferences based on what is currently known. For example, historical records and current knowledge of community ecology and biogeography lead to the conclusion that the cool temperate, moist, well-drained Central European lowlands that now support farms and villages were dense, continuous deciduous forest at the time of the Roman Empire.

Such an exercise requires considerable conjecture. For one thing, there are major disagreements about what kinds of ecosystems were located in which regions before human impact. Were the tallgrass prairies once extending from the Gulf Coast to the prairie provinces of Canada the natural ecosystem in that zone (a result of lightning-caused fires and grazing by bison) or were they created by Native Americans who burned the vegetation (and eliminated trees) to improve forage for game animals? Much the same question could be asked about lands that are now tropical savannas in northern Australia.

Likewise, while humans were spreading from Africa to other parts of the world, contemporaneous climatic changes were occurring which could also have caused biotic changes. While the importance of climate change in determining ecological patterns must be recognized, coincidence between North American large mammal disappearance and the rapid advance of humans possessing potent new hunting tools suggests anthropogenic factors played some part. There is evidence that similar mass extinctions of mammals and birds occurred at quite different times shortly after humans colonized South America, Australia, Madagascar, New Zealand and Polynesia.

Megafuana extinctions of this magnitude did not occur in Africa and Asia, where early humans resided long before they invaded the lands listed above. Roughly 19% of the large mammalian genera in Africa were extinguished compared with 74-86% in North America, South America and Australia (Martin, 1986). Presumably, human capabilities evolved slowly enough during the early Pleistocene to allow most of the giant animals of Africa and Asia to persist. By the time Homo sapiens arrived in the Americas, Australia and various islands, they were far more effective at hunting large prey. This would explain why some African and Asian elephants remain, but no North American mammoths or mastodons.

Except for changes wrought by man-made fires, the major impact of pre-agricultural people was probably on the species they hunted for food and those species that competed with humans for prey. Most other major ecological changes between the evolution of the genus Homo and the first agriculture probably resulted from changing climate.

What did the world's biota look like before human impact? Not surprisingly, it was a lot richer. North America, for example, hosted glyptodonts (an ox-sized armadillo-like mammal), giant ground sloths, several kinds of proboscideans (elephant-like mammals), a giant deer (Cervalces sp.), large camels, large musk-oxen, horses, a lion (Panthera leo atrox), a sabre-tooth tiger (Smilodon fatalis), a powerful, short-legged wolf (Canus dirus), a gigantic short-faced bear (Arctodus simus), and a bear-sized beaver (Castoroides sp.) (Kurten, 1988). Steller's sea cow grazed subtidal algal pastures from California all the way to the Aleutians and across to coastal Siberia. In the first centuries after humans arrived from Asia via unglaciated areas in Alaska, these megamammals were swept away with lightning speed. By 10,000 years ago, all these animals were extinct (Martin, 1986) except the sea cow, which held on in its last remote island redoubt in the Bering Sea until 1768.

Until the coming of the Europeans, highly diverse eastern deciduous forests of very large oak, chestnut, beech and maple reached from the Atlantic to beyond the Mississippi, and were home to billions of passenger pigeons, along with wolves, mountain lions, elk, moose, a few bison and, in the South, ivory-billed woodpeckers and Carolina parakeets. Eastern rivers ran thick with Atlantic salmon. The vast tract between the semi-arid shortgrass prairie and the eastern forest was lush, tallgrass prairie; California's Central Valley was a rich grassland, as were many of the semiarid western areas that are now sagebrush or mesquite-covered desert. Bison, elk, wolves and grizzly bears ranged throughout most of these western grasslands. The Pacific Northwest was solidly cloaked in diverse coniferous forest whose largest trees reached nearly 400 feet tall and 20 feet in diameter; California condors ranged from Mexico to British Columbia.

South America, Europe, North Africa, temperate Asia and Australia were markedly different as well. South America and Australia lost an even higher percentage of their large mammal genera than North America (Martin, 1986). Europe had a glacial fauna of megamammals nearly as spectacular as those of North America (Fenton et al. 1989); woolly mammoths (Mammuthus primigenius), woolly rhinoceroses (Coelodonta sp.), bison (Bison bonasus), aurochs (wild oxen, Bos primigenius), a giant deer (Megaloceros), reindeer (Rangifer tarandus), cave bears (Ursus spelaeus) and cave lions (Panthera leo spelaea) were among the large representatives, but extinctions were more gradual and proceeded from south to north.

After the glaciers retreated, Western Europe was densely forested from the North Sea to the Mediterranean; the Mediterranean stunted shrublands did not yet exist. Much of the Ukraine and southwestern Russia was grassland. Much of North Africa and Ethiopia was forest or tree savanna; the Sahara was much smaller. The foothills of the Himalayas and the lowlands of eastern China and Japan were covered with broadleaf forests that were even richer than their North American counterpart. From India and Sri Lanka, across southern Asia to Indochina and the Philippines, Indonesia, New Guinea and northeastern Australia, a great diversity of tropical forests prevailed. As in the other continents that were settled by advanced human cultures, the megafauna of Australia were seriously depleted; 19 out of 22 genera of large mammals vanished.

Island fauna have undergone even more drastic change. The Canary Islands had an extremely rich endemic flora; Madagascar was largely covered with forest and tree savanna and hosted a remarkable assemblage of endemic lemurs and the 1100 pound flightless elephant bird (Aepyornis maximus). This, the largest bird that has ever lived on Earth and laid eggs holding more than two gallons, survived until about 1700 (Day, 1981). Densely forested New Zealand, too, had an extraordinarily rich endemic avifauna including 20 species of giant flightless birds (the moas), the largest of which reached 13 feet in height. The isolated, densely forested Hawaiian islands hosted the most endemic biota found anywhere in the world.

III THREATS

A RESPONSES TO HUMAN IMPACTS

Human actions threaten all levels of biological diversity. The most visible level should be ecosystem diversity, but limitations on human spatial and temporal horizons make it difficult to comprehend changes occurring on this level. The magnitude of ecosystem destruction is made more visible by technological innovations such as satellite imagery; the remarkable Landsat photographs between 1973 and 1988, for example, show rampant deforestation in Brazil's state of Rondonia (see National Geographic, 1988). Less visible but better appreciated is destruction of species; it seems images of vanishing condors and elephants elicit more human response. Least visible and least understood is the loss of genetic diversity.

Human activities reduce **genetic diversity** in at least three ways. Anthropogenic disturbances can 1) eliminate whole populations of organisms and their entire genetic complement; 2) reduce population sizes to the point where genetic drift overtakes natural selection as the dominant evolutionary force; and 3) create new selection pressures.

Each species is comprised of one or more relatively distinct populations of interbreeding individuals. Genetic distinctions may arise between populations because some kind of barrier diminishes or prevents genetic exchange between organisms of the same species. As a result, individuals within one population may possess versions of genes (alleles) that are absent in another population, or they may possess the same alleles in different frequencies. The different alleles that code for varied expressions of a particular trait provide the raw material for evolution. Some combinations of alleles, called co-adapted gene complexes, are particularly important because, as a group, they confer adaptation to local conditions.

Many people do not understand the importance of preserving populations. If marbled murrelets (a species of small seabirds) still abound in Alaska, they wonder, why should we worry about their elimination in California? They fail to recognize the genetic diversity at stake. As Paul Ehrlich (personal communication) and others have pointed out, humans are causing the extinction of populations at a rate far greater than the extinction rate for whole species. As populations disappear, their distinctive alleles and co-adapted gene complexes are lost, as are the products and ecological services that populations provide. The Endangered Species Act of 1973 appropriately recognized that populations merit conservation even if they are not morphologically distinct enough to be called subspecies.

Populations which are not driven entirely to extinction, but which are stressed enough to dramatically reduce population size, may be further affected by genetic drift. Genetic drift is the change in the frequency of various alleles caused by random chance rather than by selection pressure. In small populations, genetic drift can become more important relative to the natural selection that tends to maximize the fitness of individuals, because certain individuals contribute disproportionately to the gene pool of succeeding generations by pure chance. This can result in the loss of beneficial (or detrimental or neutral) alleles, and in the fixation of detrimental (or beneficial or neutral) alleles. Thus, this non-Darwinian form of evolution can reduce genetic fitness and diminish the potential ability of an organism to withstand change.

Additionally, human activities can reduce genetic diversity by altering selection pressures. Living things evolve (i.e. their gene frequencies change) in response to selective pressures and opportunities in their environments. Anthropogenic influences have created new selection pressures.

Examples are abundant. Before the industrial revolution, virtually all peppered moths (Biston betularia) in Europe were light ashy gray matching the lichens and tree trunks on which they rested. As Europe industrialized, sulfur oxides emissions from coal killed off lichens, and the tree trunks turned black with soot. The peppered moths that survived in heavily polluted areas were also sooty black. Light-colored individuals made easy prey for birds, and were selected against.

The aurochs, the ancestor of domestic cattle, was a large, powerful, fierce creature capable of living through the rigorous European winters. Domestication by humans selected against many behaviors, and many strains of domestic cattle have lost their ancestors' abilities to find food covered with snow and to eat snow to obtain water. The aurochs and the genes that produce such adaptive behaviors are now extinct.

When first introduced in the 1940s, the pesticide DDT was hailed as the savior of the many millions of people who would otherwise die each year of insect-borne diseases such as malaria. DDT, however, selected out the most susceptible individuals, leaving less susceptible ones to pass on their genes. Now the mosquito vectors of malaria are resistant to DDT and many other pesticides, and malaria affects hundreds of millions of people worldwide.

The ancestors of modern-day corn were Middle-American perennial grasses which scattered their small production of seed each year. Today's highly selected annual corn produces huge crops of seed and then dies each year, but is unable to reproduce without human help. The seeds stay attached to the corncob, so any cobs that escape harvest produce densely crowded seedlings that cannot avoid severe competition. This would quickly lead to extinction if humans did not remove and disperse them. The ancestors of corn were long thought to be extinct until a handful were discovered in the late 1970s.

Human contact has intentionally or unintentionally altered gene frequencies in all these organisms, increasing some genes at the expense of others. Some organisms have prospered; corn plants and cattle are undoubtedly more abundant than their ancestors were. Many species, including some that we consider "wild" such as house sparrows, head lice, dandelions or coconuts, undoubtedly would be much rarer if humans disappeared. Far more have not prospered from the advance of humans, and very large numbers of genetically distinct populations and their genes have disappeared entirely.

As species are stressed, they either disappear in parts of their range, become less numerous throughout the range, or both. Local extirpation and rarefaction are both preludes to extinction. As people have an easier time recognizing species as distinct entities (as opposed to genotypes or ecosystems), it is easier to estimate the rate at which they are being lost even if, for reasons Edward O. Wilson (1986) makes clear, quantifying worldwide extinctions is very imprecise. Species' extinction is not really a process distinct from loss of populations, but rather, is its end point. When the last population of a species disappears, the species is extinct.

Like the loss of genetic and species diversity, loss of **ecosystem diversity** is a graded phenomenon. Its endpoint, however, is not as clear as with the loss of alleles or species because the definitions of ecosystem boundaries can be arbitrary.

For example, the tropical forest ecosystem is readily separable into different biogeographic regional types (such as Neotropical, Ethiopian, Oriental and Australasian), each of which can be further subdivided. Within the Neotropics, the Central American forests extending west of the Andes are fairly distinct from forests of the Amazon Basin or of southeastern Brazil. Within the Central American/Pacific Coast forest region, forests can further be divided into evergreen wet and moist lowland forests, (and into mangroves, seasonally flooded, montane and cloud forests, seasonally dry deciduous forest, and usually dry thorn forest). The classification continues within these categories, and all of these are distinct tropical forest ecosystems. There are no distinct boundaries between them to facilitate the assessment of loss at the ecosystem level.

Despite these uncertainties, some observations are clear. The organisms that compose communities in all ecosystems have mechanisms that allow them to resist some mild stresses and to recover from some stronger stresses, unless conditions change beyond a certain point. In the Klamath-Siskiyou region of southwest Oregon and northwest California, a seasonally dry area that has been densely forested for at least thousands of years, traditional, natural stressors tended to kill a mosaic of patches or individual trees and other organisms but did not transform entire forests. Large tracts of forest create a moderate microclimate that favors their perpetuation, enabling these systems to resist stress. Trees recolonize the semi-open areas that offer better opportunities than those in deep shade. These systems are resilient in the face of natural stressors of usual magnitude.

Anthropogenic stresses, however, can create a different pattern. Clearcutting eliminates the moderate microclimates which foster resilience; clearcuts can be hotter, colder, drier and windier, and thus prevent establishment of seedlings of even drought-tolerant trees. Despite repeated plantings, clearcut forests often do not begin recovery for at least decades. Even with all the advantages foresters can provide, clearcutting alters the physical conditions so much that it pushes the system beyond its ability to recover except during unusually cool, wet years or multiyear periods.

B DETERMINANTS OF VULNERABILITY

The eastern elk that once roamed the land east of the Mississippi are now extinct (Thomas and Bryant, 1987), but white-tailed deer are more abundant than ever. Only a few thousand spotted owls survive in the Pacific Northwest, but barred owls have invaded and are spreading throughout their range (Norse, 1990). Amazonian upland terra firme forests are disappearing even faster than nearby floodplain varzea forests (Low, 1984). Although fewer than 20% of the world's birds occur on islands, more than 90% that have become extinct in historic times are island species (Low, 1984). These situations raise the question: What determines the vulnerability of particular genotypes, species and ecosystems?

There has been remarkably little research into most aspects of vulnerability. As is typical in discussions concerning biological diversity, most attention has been directed towards losses at the middle level (species extinction), but differences in vulnerability among genotypes within species and among ecosystems must also be considered.

Some differences in vulnerability are inherent; the organisms or ecosystems would be more vulnerable whether their stressors were natural or anthropogenic. Others result largely from the nature of anthropogenic influence.

Most important insights concerning vulnerability have been drawn from studies of island species, from both oceanic islands (those always isolated from land) and from land bridge islands (those cut off from mainlands, often as a result of post-glacial sea-level rise or creation of reservoirs). Some factors that determine vulnerability in species are correlated. For example, many species of large organisms have small populations, but small population size is a major determinant of vulnerability regardless of organism size; conversely, large size can make a species vulnerable independent of its initial rarity.

1. Determinants of vulnerability among species

a) Small effective population size. All else held equal, small populations are more vulnerable than large ones for a variety of reasons (Frankel and Soule, 1981). Some are demographic (e.g. unbalanced sex ratios) which are more likely in smaller populations; short of resorting to hybridization, there was no hope of perpetuating the dusky seaside sparrow when the population fell to five individuals, all of which happened to be male (Cade, 1983).

Demographic vulnerability is not merely a question of the sex ratio, but of the number of breeding males and females (connoted by "effective" population size). Grizzly bears in the greater Yellowstone ecosystem number perhaps in the 200s, but many are too young or too old to reproduce. The effective population size is much lower because only 30 or so are reproductive females. Thus, age structure is a second key demographic variable that can render small populations vulnerable.

Furthermore, populations fluctuate in response to environmental variables that might or might not be obvious. A large population can lose 90% of its individuals and still have a good chance of recovery if its habitat remains intact. Conversely, normal fluctuations in a small population can lead to demographic imbalance and extinction. Some groups, such as butterflies (Ehrlich, 1983) might be particularly vulnerable to demographic fluctuations leading to extinction.

Additionally, there are genetic reasons why small populations are vulnerable (Schonewald-Cox et al., 1983). Smaller populations are less likely to possess rare genes. As conditions change, rare genes may confer improved fitness (the improved ability to reproduce successfully). The presence of rare genes can be a vital form of evolutionary insurance, thus their absence makes a species more vulnerable. Additionally, small populations are subject to genetic drift, as previously discussed. Genetic drift can diminish fitness (Franklin, 1980).

Rarity exists for many reasons, including some which are simple consequences of high species diversity (Cody, 1986); thus rarity per se is not always harmful for a species. Some naturally rare species have special mechanisms allowing persistence at low densities (Rabinowitz et al., 1984). However, formerly common species which have been artificially reduced are much less likely to possess mechanisms such as these.

Small population size, especially in a population whose numbers have been recently reduced, is probably the most important risk factor for extinction (Terborgh and Winter, 1980). Countless species have had their populations reduced by human activities.

b) **Narrow geographic distributions.** Abundance is determined by a combination of three factors: 1) size of geographic range, 2) number of utilized habitats; and 3) individual population size (Rabinowitz et al., 1986). A species can be termed rare by deficiency in any of these factors. Species such as western red cedars and mountain lions have broad geographic distributions and occur in many kinds of habitats but typically have low densities. Others, such as red mangroves and canyon wrens have broad geographic ranges but occur only in rare, localized habitats. Still others, such as Haleakala silverswords and Devil's Hole pupfish are classic endemics (species found only in a restricted area).

All other factors being equal, a narrower geographic range increases the likelihood that some natural or anthropogenic stressor may cause extinction. Human proliferation has significantly reduced the geographic range of a great number of species.

c) **Large area requirements.** Species of large organisms need more resources than small ones, and tend to range widely to find them; other species depend on resources that are widely scattered over a large area. Species such as these are vulnerable to any stressor that decreases the size of their habitats. Grizzly bears, spotted owls, and Florida panthers are currently endangered because ranching, logging, and housing development have eliminated most of their habitat and isolated them in small, island-like refuges.

d) **Specialization.** Specialists requiring a particular type of habitat or food are especially vulnerable. One famous example is the Everglade snail kite (Rostrhamus sociabilis), a species endangered due to its dependence on a single prey, the apple snail (Pomacea paludosa) (Takekawa and Beissinger, 1989). As the hydrology of the Everglades has been altered for agriculture and housing development, apple snail habitat has disappeared and the monophagous raptor has diminished. Many specialists have decreased as a result of human activities.

e) **Intolerance of disturbance.** Both the frequency and type of disturbance occurring in natural ecosystems exert enormous influence on plants, fungi and animals. In general, disturbances increase populations of species that are able to tolerate disturbance or take advantage of the newly available resources in recently disturbed areas. Many of the these are opportunistic, "weedy" species, such as dandelions and the red imported fire ant, which devote a relatively large percentage of their biomass to reproduction and produce many young (r-selected species). In a climax community, these are often kept in check by competition with species which devote more energy to the growth and maintenance of the adult (K-selected). Disturbance shifts the scales, and "weedy" opportunists flourish while climax species such as the western red cedar, myotis bat, and the northern spotted owl, disappear.

f) **Large size.** Species of large organisms often have small populations and large area requirements, but they can be vulnerable for other reasons as well. This might seem counterintuitive, as large size can confer resistance to forces that harm smaller individuals. For example, giant sequoias have very thick bark that makes them virtually immune to the frequent fires that kill many thinner-barked trees.

However, many forces select against large species, (e.g. wind which selects against the tallest trees, and predators, which often take the largest prey they can readily handle); (see Connell, 1975). Humans, too, tend to hunt large prey (such as deer) and log tall, large-diameter trees (such as sugar pines); humans are especially likely to discriminate against large species because modern technology can diminish any natural advantages conferred by large size, while our economics demand that we maximize return for unit effort by taking the largest individuals possible. That is why blue whales were pushed towards extinction before the smaller fin whales, which were depleted before the still smaller sei whales, which were hunted to low levels before killing commenced on the smallest baleen whales, the minkes (Ehrlich et al., 1977).

g) **Slow reproductive rate.** There is enormous variability in rates of reproduction. Two species can have equal abundance if one reproduces faster but the other has lower mortality. If conditions change so that their mortality rates become similar, the faster reproducer will be better able to recover from disturbance. Faced with increased mortality from off-road vehicles, desert tortoises are hindered by their inability to reproduce until they reach 12-20 years old (Campbell, 1988). A look at the Endangered Species List will show many species with unusually low reproductive rates.

h) **Evolutionary naivete.** Organisms which evolved in isolation from competitors, predators, or diseases are more vulnerable. This is most obvious with island species such as plants lacking physical or chemical defenses against grazers, or defenseless birds such as the kakapo (Strigops habroptilus), a very large, flightless, ground-dwelling and critically endangered parrot from New Zealand.

Similarly, anthropogenic stresses can render even mainland species "naive". Striped skunks and adult eastern box turtles have evolved natural defenses to protect themselves from foxes, cougars, black bears and many other natural predators, but not from speeding cars. Many species are defenseless against man-made chemicals in their environments. Industrial wastes, insecticides and herbicides can jeopardize many species--perhaps most except herbivorous insects--that are not adept at breaking down novel substances into non-toxic ones.

i) "Amphibious" habits. "Amphibious" organisms, whose life cycle or habits require more than one type of habitat, run greater risk of losing one of these habitats to natural or anthropogenic disturbance. The vertebrate class Amphibia is hardly alone in this; "living double (or multiple) lives" is very widespread. Nevertheless, this is one of the less-discussed determinants of vulnerability among species. Reed Noss (1987) notes:

> Field naturalists recognize that many animal species require distinctly different habitats for different activities or separate stages of their life cycles. Some organisms, such as holometabolous insects [those which undergo complete metamorphosis] and many amphibians, undergo ontogenetic niche shifts [shifts related to development] that place them in drastically different habitats after metamorphosis.... Other organisms... commute between different patches or community-types to meet life history needs.

In the class Amphibia, the most familiar life history is exhibited by spotted salamanders; adults live in moist places on land but lay eggs and undergo larval development in water. This species is vulnerable to either elimination of the large fallen logs under which they hide--which happens in intensively managed forests--or from pollution of their breeding ponds from acid rain.

Migratory species are also amphibious, whether they move seasonally between uplands and lowlands, as do mountain goats and some elk populations, or migrate long distances, as do hundreds of bird species that breed in north temperate zones but winter in tropical regions. Many populations of migratory songbirds seem to be decreasing, but whether this decrease is due to loss of their tropical forest wintering grounds, to pesticide poisoning in their North American summer grounds, or to some other factor or combination of factors, remains to be determined.

Marine mammals require two media. Whalers did not have to search the nearly opaque depths; they only needed to wait until their quarry surfaced to breathe. Many materials such as spilled oil collect at the land-sea interface, providing obstacles for a number of functional groupings, including neuston, pleuston, birds that rest on the sea surface and any underwater species that must surface to breathe. Sea turtles further add to their vulnerability by laying eggs on land, where they must contend with destruction of nesting beaches (for example, by the building of seawalls), egg predation (especially by humans) and light pollution (which disorients young that hatch at night, preventing them from reaching the sea).

Less obvious examples exist. Insects that metamorphose and plants that reproduce sexually often have very different behaviors and habitat requirements in different life history stages. Adding these to the more obvious species with double lives leads to the conclusion that most species are amphibious to at least some degree. Certainly, not all are threatened, but the more different the phases, the greater the likelihood that at least one of the phases will be affected by human activities and thus affect the population dynamics of the species.

2. Determinants of vulnerability among sub-specific populations and genotypes

Each of the variables discussed above may also operate on different populations of a species; e.g., tundra populations of marbled murrelets (Brachyramphus marmoratus) are far less vulnerable than the populations in California, Oregon and Washington, which nest only on the mossy limbs of ancient conifers, a habitat that is fast disappearing (Marshall, 1988). These murrelet populations are equally amphibious, but only the resource needed by more southerly populations is severely limiting.

Beyond this, broad principles about genetic determinants of fitness among individuals do not seem to be well defined. Genes that confer the ability to reproduce early would greatly increase fitness in a species being heavily exploited by humans. As Power and Gregoire (1978) have noted, this type of selection affects lake trout (Salvelinus namaycush) in a lake in Quebec having landlocked harbor seals (Phoca vitulina). Compared with similar nearby lakes lacking seals, trout in the lake having seals reproduce much earlier and have far more eggs per gram of body weight, apparently because seals are especially adept at preying on trout that are massed for reproduction. This strongly selects for semelparous (big bang) reproduction.

Similarly, nonmigratory genotypes would be favored in populations which are genetically polymorphic for migration if humans eliminate one of the habitats between which migrators move. Genes coding for fear of humans, tolerance of toxic chemicals and the ability to switch to abundant hosts (such as corn plants) would also be selected for in human-dominated habitats, and genotypes lacking such traits would fare less well.

3. Determinants of vulnerability among ecosystems

a) **Impermanence.** All places on the Earth's surface change in ways which alter the conditions for their communities, but these changes occur on diverse timescales. Much of the deep seabed might survive undisturbed for more than a hundred million years, until seafloor spreading draws it into subduction zones. Many other ecosystems change orders of magnitude faster. Some ecosystems are inherently short-lived because the physicochemical factors shaping them are ephemeral; deepsea hydrothermal vent communities appear to last only decades, as long as the upwelling flow of mineral-rich heated water. When the flow stops, the tubeworms, mussels and other vent fauna die.

Unlike this example, most ephemeral ecosystems are actually successional stages; succession drives, or at least hastens, the changes. Ox-bow lakes in fertile floodplains are also short-lived, filling in quickly as succession proceeds from river to lake to marsh to forest or prairie. In exceptionally short-lived ecosystems, many species are opportunists that colonize and disperse readily under natural conditions to other new ecosystems of the same kind. As long as something resembling the natural disturbance regime is preserved, these successional stages will persist.

A number of human activities intentionally or incidentally diminish the frequency of disturbance. Fire suppression in forests, for example, favors mid-successional and sometimes late successional species at the expense of early successional species.

b) **Oligotrophy.** Ecosystems in which nutrient elements are scarce and limiting to many organisms (termed oligotrophic ecosystems) are vulnerable to changes in nutrient availability. Tropical wet forests on old, weathered soils are often nutrient-poor because rain has long since leached key nutrients below the rooting zone. Many freshwater lakes and streams (including streams in caves) are nutrient-poor, as are the non-upwelling coastal waters off arid regions and the vast majority of the open ocean (non-upwelling areas) from the surface to the seabed.

Countless nutrient-poor lakes have undergone eutrophication (nutrient addition which disrupts the ecological balance) from nutrient-rich discharges and runoff. In Key Largo, Florida, an area which has undergone rapid development in recent years and which receives an ever-greater amount of nutrients from the Miami metropolitan area to the north, reef corals have been suffering high rates of overgrowth from algae which grow faster than corals under eutrophic conditions.

In a smaller number of cases, ecosystems are also vulnerable to anthropogenic decreases in nutrient availability. The estuarine lakes at the mouth of the Nile once supported rich fisheries because annual Nile flooding provided large, predictable inputs of nutrients. The completion of the Aswan High Dam trapped the nutrients in Lake Nasser, eliminated this flooding and quickly eliminated the fisheries in the estuarine lakes (Shaheen and Yousef, 1979). On land, pH markedly changes the availability of various nutrients by affecting both ion exchange capacity and the amount of nitrogen fixation in soils. Acid precipitation can alter the species composition of an ecosystem by altering nutrient availability.

Oligotrophic ecosystems might be more vulnerable than eutrophic ones, however, because more human activities accelerate nutrient release than decrease it. A more general principle is that anything that affects an ecosystem's inputs, outputs and internal cycling of nutrients can cause profound changes because nutrient availability is among the most important factors shaping the evolutionary strategies of organisms, the outcome of competitive interactions and the functioning of ecosystems.

c) **Undersaturation.** All ecosystems are to some degree vulnerable to invasion, but oceanic islands and isolated lakes (such as desert springs and glacial lakes) are particularly vulnerable. Their biota is typically undersaturated, exhibiting far fewer species than might otherwise be present. This creates the previously mentioned evolutionary naivete in isolated species, allowing them to be easily exploited by introduced species. The addition of rats, cats and goats to islands, and of trout, blackbass and Nile perch to lakes where they were not native has had devastating consequences for native species composition, structure and functioning in these ecosystems. Among the many examples are the severe effects of introduced rabbits on the vegetation of Laysan Island, and the elimination of six out of eight common, native fishes of Panama's Gatun Lake by an introduced predatory cichlid, the peacock bass (Cichla ocellaris) (Zaret and Paine, 1973).

Not all undersaturated biotas are islands or isolated lakes, however. The reason for undersaturation in some cases is historic. Southern Florida has a quasi-tropical climate, and would undoubtedly support far more tropical species had they not been wiped out during glacial periods when the region was cooler. Species that found their way from warmer areas since the last glacial retreat have prospered there, as have large numbers of alien species recently introduced by humans (Courtenay, 1978).

d) **Isolation**. Isolated ecosystems of any kind are vulnerable because the extinction of species within them is not fully offset by colonizations from outside. Hence, isolated ecosystems tend to have fewer species compared with extensive examples of the same kind of ecosystem (MacArthur and Wilson, 1967); the more isolated the ecosystem, the fewer species it will have.

Brown (1971) found that for non-flying mammals confined to isolated western mountaintops, the number of species on a mountaintop is determined solely by extinction rates. There is no recolonization across climatically unsuitable lowlands. While natural processes have always left isolated ecosystem patches here and there, anthropogenic habitat fragmentation, due to agricultural lands, roads, dams, cities, clearcuts and tree plantations, has dramatically increased the fragmentation, and hence the isolation, of ecosystems worldwide.

e) **Small size**. Other things being equal, small ecosystems have fewer species than large ones, partly for reasons described above in the discussion on species with large area requirements. Additionally, many external influences penetrate only a finite distance into ecosystems. In closed canopy forests, nest predators, brood parasites (Wilcove et al., 1986), and hot, dry winds penetrate within the border from one to hundreds of meters. As a result, edges are unsuitable for forest interior species. In a very large patch, the fraction that is edge will be negligible, but the fraction increases rapidly with decreasing patch size until the entire patch is edge (Franklin and Forman, 1987). The fragmentation that is isolating ecosystems from sources of recolonization is also decreasing the size of remaining fragments, decreasing population sizes, increasing the amount of edge and increasing extinction rates.

f) **Proximity to human populations.** This is by far the most important risk factor for ecosystems, as witnessed on any intercontinental flight. Where water is not limiting, essentially all level, fertile land is agricultural except for areas where towns and cities have succeeded farmland. Only on steep slopes are there remnants of the original forests or grasslands; in the most crowded lands, even these marginal lands are farmed. Similarly, in dry lands, the same riparian strips which once supported disproportionately large numbers of animals and plants, now support farms, livestock operations and towns.

A few things that humans consume (most underground minerals, for example) show little correlation with biological diversity. More often, however, the same physical factors which favor vibrant communities of living things also favor humans, and Homo sapiens has appropriated these habitats for its use. Since the best lands are already long gone, almost all new colonization is now on lands that cannot support dense human populations on a sustainable basis. This often does not stop desperate people from moving there anyway.

Humans actions may also threaten ecosystems located downwind and downstream of human activities. The acidification of hundreds of lakes in eastern North America by emissions of power plants far upwind and the contamination of estuaries with polychlorinated biphenyls released far upstream are two examples

C THE ULTIMATE CAUSES

At first glance, current threats to biological diversity appear many and varied. The toxins washed from a tobacco farm into a Kentucky stream and the expansion of Masai cattle herders onto the last available Kenyan virgin grassland might seem to be localized manifestations of different problems, but they are not. The use of potentially hazardous chemicals to increase crop yield to feed an ever expanding human population, and the continued conversion of wildlands for human use are different symptoms of the same underlying condition and their effect is cumulative. Reduced to its simplest terms, environmental impact is primarily the product of two trends: the exponential growth of the human population and the increasing per capita consumption of the Earth's resources to provide for human needs.

Unchecked population growth is a driving force which pushes developing nations into a self-perpetuating cycle of economic disaster and environmental degradation. Those same nations which are now teetering on the edge of environmental and economic disaster--manifested in devegetation of the land, mass extinctions, crushing foreign debt, skyrocketing inflation, decreasing per capita income, increasing infant mortality, decreasing life expectancy and chronic insurgencies--will have twice as many mouths demanding to be fed in 25-35 years. In Kenya, this figure is only 17 years.

Some nations have avoided the later symptoms of overpopulation because their land is so inherently rich that species, soils and water supplies have not yet been exhausted. Others have avoided excessive environmental degradation and natural resource depletion by externalizing their environmental impacts; they disperse their wastes to areas down-stream or down-wind and import food and raw materials. In these nations, living standards and per capita consumption of natural resources are high and even increasing, making per capita environmental effects much higher than in impoverished countries; The United States, for example, has 320 times as many cars per capita as India (Ehrlich and Ehrlich, 1988), and thus consumes far more fossil fuel, steel, aluminum, coal, land, water and air.

D THE PROXIMATE CAUSES

These ultimate causes of anthropogenically-driven biodiversity loss are manifested in numerous proximate causes, which have been summarized here under six headings:

1. Direct population reduction (intentional and incidental taking)

Throughout most of its existence as a species, Homo sapiens has subsisted by foraging for roots, fruits, insects and the occasional bonanza of a dead or dying mammal. Technologies were too primitive to allow early humans to prey on healthy individuals of the huge Pleistocene African mammalian species. Over time, an increasing sophistication at tool-making, an ability to control fire, and an improved ability to communicate have shifted the balance in Homo sapiens' favor.

Before the 1600s, blue bucks could be killed only by people within the range of a cast spear. After the Dutch and their firearms arrived in South Africa, these antelope could be killed from much greater distances; the last blue buck was shot about 1799. Two centuries ago, it took a team of Pacific Northwest Native Americans days to fell a giant western red cedar, the only tree they could split for planking to make their houses. Moving trees away from the rivers was beyond imagining. Today one lumberjack armed with a chainsaw can down a forest giant in minutes, and powerful machines can move and mill any tree species and ship the logs or lumber across the ocean to Japan. Our ancestors could fish only in shallow waters, and could take few fish at once. Today, powerful, fossil-fueled, air-conditioned ships electronically locate schools and harvest fish in nets vastly larger than the mouths of the predators with which the fishes evolved.

There is great diversity in what humans seek from nature, how it is acquired, and the degree to which humans restrain themselves from overexploitation. Some direct exploitation of living things, such as the sport hunting of bighorn sheep in the western United States, is carefully controlled and monitored. (However, see Irby et al., 1989 for a contrary view). With notable exceptions, most industrialized countries have gained considerable control over direct exploitation of native species. In many other nations, however, uncontrolled taking of species is still common; populations of African elephants are sharply decreasing throughout most of East Africa due to human desire for ivory. Populations of black rhinoceros have been so decimated that poachers must be deterred by round-the-clock armed guards. For many species, laws are non-existent or simply not enforced.

Non-target organisms are similarly threatened. Trappers cannot ensure their traps will snare only the intended species; a sizeable share of the organisms killed are not the furbearers that trappers seek, but other species such as skunks and golden eagles. Now that poaching of mountain gorillas in Rwanda has ended, the greatest immediate threat to these endangered apes is incidental take in antelope snares set by poachers.

Perhaps more widespread is incidental take in marine ecosystems. As much as 80-99% of a shrimp-trawlers catch can be nontarget species of fishes, starfish, crabs, stomatopod crustaceans and jellyfish, many of which die before being thrown overboard.

Shrimp trawling is a major threat to sea turtles, such as the endangered Kemp's ridley inhabiting the coastal waters of the southeast United States (Ross et al., 1989), and a threat of uncertain magnitude to totoaba (Cynoscion macdonaldi), a large, endangered endemic fish in Mexico's Sea of Cortez (Ono et al., 1983).

Driftnets up to 30 miles long, set in the North Pacific by Japanese, South Korean and Taiwanese salmon and squid fishermen, annually drown hundreds of thousands of seabirds, especially short-tailed shearwaters and tufted puffins, in addition to thousands of Dall porpoises and lesser numbers of other marine mammals (O'Hara et al., 1986). In the view of Jehl (1988), the numbers of seabirds killed are indeed high and locally significant, but the impact of drift nets on their populations is uncertain; better answers could be obtained through population modeling.

Purse-seiners locate yellowfin and skipjack tunas by spotting dolphins associated with the tuna schools. They surround the schools and unintentionally drown dolphins in their nets. In 1972, more than 423,000 small whales of 13 species were killed, mainly spotted, common, striped and spinner dolphins. The passage of the Marine Mammal Protection Act and subsequent laws have sharply curbed the killing, but it is still on the order of 20,000 for the U.S. tuna fleet alone (Jehl, 1988).[1]

In the Philippines, fishing methods reach unprecedented levels of destructiveness to non-target species. Fishing boats pulverize coral reefs with heavy weights to drive out reef fishes or collect these fishes by poisoning entire reefs with cyanide.

In recent years, the attention of conservationists has focused on other causes of declining biological diversity. In some cases, direct taking is a humane issue or an issue of sound resource management rather than a question of diminishing biological diversity. For a significant number of taxa around the world, however, intentional and incidental taking probably rank with physical habitat destruction, pollution, climatic change and alien species as major threats.

2. Physical alteration

When Europeans first settled in North America, the first species they jeopardized were those they killed for food, fiber or skins, and those they considered competitors. Since then, the most jeopardized species have become those whose habitats humans appropriate. Worldwide, in places as diverse as the tundra of Alaska's North Slope and the rainforests of Borneo, the greatest damage to biological diversity is caused by physical alteration of ecosystems.

Human beings physically alter ecosystems in several related ways. The most complete kind of alteration is conversion, the complete alteration of ecosystem structure, composition and functioning. Ecosystem conversion includes the changing of virgin

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[1] Further decrease of incidental dolphin kill is expected following recent decisions by the three largest U.S. tuna companies to produce "dolphin-safe" tuna.

prairie into cornfields, of deciduous forest into coniferous tree plantations, and of freshwater marsh into shopping malls.

The extent of conversion differs markedly from one ecosystem to the next. Between 25 and 40% of the humid tropical forest biome is gone (Erwin, 1988). Approximately 56% of former United States wetlands is gone (CEQ, 1989). Some 87% of the ancient forests in the Pacific Northwest is gone (Norse, 1990). Essentially no functioning North American tallgrass prairie remains; only a few scattered remnants exist (Nature Conservancy, personal communication with Barbara Shapiro). Weedy species have coped with these changes by moving to other ecosystems or adapting to the markedly changed conditions in situ, but the specialists requiring specific habitats have been reduced roughly in proportion to the percentage of habitat lost.

As serious as outright conversion are two kinds of partial alteration. One is ecosystem fragmentation, in which barriers to organism dispersal separate more or less intact pieces of ecosystems. The interruption of a river with a dam to create a lake, the clearcut logging of parts of an ancient forest (even if replaced by a tree plantation), or the building of a road through a salt marsh would all create barriers of this sort.

Fragmentation has been a topic of intense scrutiny since Terborgh (1974) and Diamond (1975) began applying island biogeography theory to fragmented remnants of once-continuous ecosystems. Destruction reduces the area of the ecosystem, but the remaining fragments further suffer from decreased populations and from the penetration of external physical and biological influences. Wilcove et al. (1986) provide a particularly illuminating example. Birds in isolated temperate forest fragments are subject to a much higher rate of nest predation and brood parasitism from edge species even hundreds of meters into the fragment. As a result, small fragments support fewer species of birds than would the same land area within unbroken forest.

The second type of partial alteration is the deletion of some ecosystem component or components, termed ecosystem simplification. Examples of this include the removal of standing dead trees in an ancient forest, elimination of a stream's sensitive submerged plants due to increased siltation from livestock grazing, and eagle abandonment of nesting trees due to human intrusion.

Many human activities that fragment ecosystems also simplify them; the previously discussed "edge effect" contributes to this. Intact forests are moister, less windy, and cooler in hot weather than clearcuts. In the Southeast, Seastedt and Crossley (1981) found that summer temperatures at the soil surface averaged 26°C (79°F) within forests but average 42°C (108°F) in adjacent clearcuts. When forests are fragmented, the harsher external conditions penetrate the fragments, allowing hot, dry air to desiccate forest plants, fungi, slugs and salamanders that require moist conditions.

Ecosystems with more three-dimensional structure sustain more species (MacArthur and MacArthur, 1961). A flat expanse of rock will support only species able to withstand exposure to heat, cold, rain and wind, and able to deter enemies without the assistance of shelter. The addition of boulders or trees creates diverse microclimates and refuges from stress and predators. Structural diversity provides opportunities for species that need vertical surfaces, horizontal surfaces, tangles, cavities, mating sites and observation posts. For example, a forest having a canopy but no shrub layer cannot support a hypothetical bird that forages in the canopy but nests in shrubs. Complex habitats accommodate more species because they create more ways for species to survive.

Similarly, species diversity begets more diversity. In English tree plantations, Peck (1989) showed that increased tree diversity provides increased feeding opportunities for songbirds; monocultures have the lowest diversity. Predators, too, can affect species diversity, as Paine showed in a classic study in Puget Sound. He found that removal of a top predator, the ocher starfish, decreases species diversity in the intertidal zone because it allows mussels (Mytilus sp.), the dominant competitors and preferred prey of the starfish, to monopolize the substrate (Paine, 1966). In these and many other cases, simplification, including reduction of species diversity, leads to a further simplification.

The differences between fragmentation or simplification and destruction are a matter of degree. All ecosystems have some degree of natural disturbance and occur as mosaics of different successional stages. Most communities would persist for eons if the nature, amount and timing of disturbances did not change dramatically. Anthropogenic changes, however, are quick, drastic and capable of overwhelming the abilities of species and ecosystems to recover.

3. Chemical pollution and solid wastes

If one were to take a bottle of sterile nutrient broth and seed it from a pure culture of protozoans such as Tetrahymena, the population would begin to grow rapidly. Some time later, growth would level off and finally reverse into decline, perhaps to a low level or perhaps to extinction. The Tetrahymena would unwittingly have exhausted their food supply and poisoned themselves with their own toxic waste products.

Of course, this artificially simplified system lacks renewable resources and supplementary species to convert waste products into harmless or useful substances. In nature, Tetrahymena are normally part of a self-regulating system. If they overexploit their resources, their population will decrease allowing their prey to recover. Increasing wastes become a resource for other species capable of metabolizing them and thereby rendering them safe for Tetrahymena. In short, Tetrahymena have survived because they live in a system of indefinitely renewable food supplies and indefinitely recyclable waste products.

The Tetrahymena example holds true for any population of organisms, including Homo sapiens. In the past, human waste products were resources for animals, plants and microorganisms, which converted them into usable resources, but the wastes of modern society tend to be regarded as pollutants to be removed or dispersed. The volume of wastes generated by a still growing and increasingly "disposable" society have reached overwhelming proportions in many industrialized nations, and the problem of safe waste disposal remains in many developing nations. Many synthetically produced products, chemicals and wastes are exceedingly durable and unfamiliar to organisms which traditionally break down waste, rendering them non-biodegradable; many are also toxic to living organisms. Not only are biologically important elements being wasted by failure to recycle them, but the production of substances toxic to life is further diminishing the already finite ability of living systems to break them down.

Pollution seldom destroys entire ecosystems. However, the stress of pollution can simplify the community structure within an ecosystem, thereby impairing the normal functioning of that ecosystem. Ecologists commonly assess the severity of pollution stress on community structure by measuring either reductions in overall species diversity (species-level biodiversity) or changes in the abundance of indicator species. The indicator species fall into two categories: "decreasers" (those sensitive to the pollution stress) and "increasers" (those that can tolerate the stressful conditions and expand into niches vacated by the decreasers). It is possible to generalize about observed and predicted effects of pollution on biodiversity. This discussion considers acid deposition, gaseous phytotoxicants (gases toxic to plants, specifically ozone), excessive nutrients (from fertilizer or wastewater), pesticides, plastics in marine environments, bioaccumulation of toxics, and National Wildlife Refuge contamination.

a) Acid deposition.

The biotic community structure in unbuffered lakes and streams has been heavily impacted by acid deposition. In buffered lakes and streams, low ecological effects are likely. For unbuffered wetlands, effects could be intermediate in severity. Effects on coniferous and deciduous forest ecosystems are controversial, perhaps ranking as high as those in unbuffered aquatic ecosystems though forest dieback has not yet been linked conclusively to acid deposition (EPA, 1987; NAPAP, 1988).

The effects of air pollutants do, however, ramify throughout susceptible forest ecosystems. Amphibians that breed in northeastern meltwater pools, such as blue-spotted salamanders and wood frogs, are especially vulnerable to the direct effects of acidification. Populations of other species, such as common loons and black ducks, are believed to suffer from diminished food supplies in acidified lakes. Reduction in population of still other species, such as the northern parula warblers, has been correlated with the disappearance of tree-dwelling lichens that are extremely sensitive to air pollutants (Schreiber and Newman, 1988).

b) Gaseous phytotoxicants (e.g. ozone).

Gases toxic to plants, such as ozone, are believed to have severe effects on coniferous and deciduous forests, little effect on desert and grasslands, and unknown but potentially severe effects on alpine/tundra ecosystems. In coniferous forests, the adverse effects of ozone on the ecosystem and its biotic components have been well documented. Pines grow more slowly under ozone stress and are also more susceptible to pest or pathogen attacks such as bark beetle. Dieback of coniferous forests is the result of these combined effects. Fungi and algae, in the form of lichens, are especially sensitive to air pollution and their decline can serve as an early warning that a forest ecosystem is under stress (EPA, 1987).

c) **Excessive nutrients.**

Nutrients are considered a major hazard to unbuffered lakes, a lesser threat to buffered lakes and unbuffered streams, and still less of a threat to buffered streams. Nutrients have the potential to cause major problems in estuaries and moderate problems in coastal waters (EPA, 1987).

In freshwater ecosystems, lakes, rivers, and streams, degradation most commonly takes the form of nutrient overloading. Run-off from farmlands and discharges from wastewater treatment facilities (or other point sources) can inject nitrogen and phosphorus into waterways, stimulating excessive and sometimes noxious growth of algae. When the algae die, after exhausting the nutrient supply or from simple overshading, their products of decay remove oxygen from the water and cause suffocation of fish and other aquatic animals. The technical term for such unwelcome enrichment is "eutrophication". Fish, insects, and submerged aquatic vegetation (and other primary producers) may be threatened by accelerated eutrophication in freshwater ecosystems.

Estuaries are especially vulnerable to eutrophication. At the interface between freshwater and marine systems, estuaries trap nutrients that contribute to their high productivity but can cause eutrophication. Receiving the outflow of entire watersheds and nearby cities, the estuaries may be victims of toxic loading as well. In areas where human waste and other organic material are dumped directly into waterways, the threat to human health is obvious but there is also the danger that aquatic organisms will be killed by the oxygen demand of the waste (as is the case with the algal die-offs mentioned above). Fish, shellfish, and many other groups in the estuarine community may be seriously reduced by nutrients and related pollutants. Seagrass and coral reef communities are very seriously threatened by excessive nutrient and organic loading. It is also possible that a connection exists between nutrient discharges and blooms of noxious red or brown algae. These "red tides" seem to be increasing in many coastal areas and could also be benefitting from global warming (Brower, 1989).

The oligotrophic (nutrient-poor) characteristic of coral reefs is easily upset by enrichment from sewage or runoff from fertilized agriculture. Discharge of sewage into Kaneohe Bay, Hawaii has dramatically changed the rocky benthos from a coral reef ecosystem to one dominated by green filamentous algae (Steven Smith, University of Hawaii, personal communication). The addition of limiting nutrients favors both phytoplankton blooms, which lower benthic light levels, and fast-growing soft algae, which smother and shade out corals.

d) **Pesticides.**

Pesticides or herbicides applied in freshwater or estuarine ecosystems could have high ecological impacts but effects in wetlands are uncertain. Also uncertain are the effects of biocides (substances destructive to many organisms) applied in terrestrial ecosystems on those ecosystems or nearby aquatic ecosystems. Pesticides can, however, have major impacts on biological diversity in agroecosystems, reducing the abundance of many beneficial insects and other non-target organisms (EPA, 1987). The repeated application of pesticides selects out unresistant strains of pests.

Pesticides can vary widely in toxicity, specificity, persistence and bioaccumulation. Pesticides which lack specificity can have harmful effects on a wide range of target and non-target organisms, and can decimate populations of a "pest's" natural predators. Though the use of some pesticides which are highly toxic to wildlife has been banned in the U.S. (e.g. DDT), legal pesticides (e.g. diazinon, chlorpyrifos) continue to harm wildlife through correct and incorrect usage (National Pesticide Telephone Network, personal communication; Daniels, 1989), and dangerous pesticides which have been banned in the U.S. are still produced in the U.S. for export. Wildlife can be endangered through lawn care use of pesticides as well as agricultural use; homeowners are more likely to overuse chemicals, using 10 times more per acre than is used on agricultural land. Songbirds may be particularly at risk. (Levy, 1989).

e) Plastics in marine environments.

The United States produces some 50 billion pounds of plastics per year. Much of what does not wind up in landfills is dumped or washed into the sea, in the form of lost crab pots, torn gill nets, discarded strapping, garbage bags, bottles, tampon applicators and six-pack rings. These strong, durable materials entangle or are ingested by marine mammals, birds, turtles, fish and others, killing, for example, some 30,000 northern fur seals per year (O'Hara et al., 1988). They pose a very serious threat to offshore and nearshore marine mammals and birds, and nearshore reptiles (turtles). Although U.S. law now prohibits ships from dumping plastic trash, and the plastics industry is making significant moves toward limiting marine plastics pollution, this remains a serious problem in marine environments due to land-based litter, and difficulty enforcing the dumping ban.

f) Bioaccumulation of toxics in mammals.

While the effects of acutely toxic chemicals are often obvious, many substances do not cause immediate lethal effects but can reach toxic levels in organisms (or adversely affect their reproduction) through long-term accumulation. Organisms feeding at or near the top of the food chain, such as large mammals and predatory birds, are often at greatest risk. Beluga whales living in the Canada's St. Lawrence River have developed immune system suppression, bladder cancer, hepatitis, bronchial pneumonia and perforated ulcers related to the more than 30 hazardous contaminants found in their bodies (Shabecoff, 1988). Included are levels of polychlorinated biphenyls (PCBs) high enough to classify the whales carcasses as toxic waste under Canadian law. PCB contamination has been implicated in the unprecedented die-off of at least 740 dolphins along the Atlantic coast in 1987/1988 (McKay, 1989).

g) National Wildlife Refuge Contamination.

A 1985 survey by the Fish and Wildlife Service (FWS) identified 85 of the nation's 430 National Wildlife Refuges as potentially contaminated by agricultural drainwater or by municipal, industrial or military activities. Investigation of the Refuge System, the only federal lands managed primarily for wildlife, was sparked by the discovery of chemical contamination in the Kesterson Refuge, which caused the death of approximately 1,000 ducks between 1983 and 1985. A 1987 GAO report indicated that FWS had not adequately investigated the issue, and that contamination may be even more widespread than FWS reported. (GAO, 1987).

4. Global atmospheric change (climate, UV-B and CO_2)

Most threats to biological diversity affect some areas intensely, but not others. The alteration of the composition of the atmosphere by the addition of trace gases, however, threatens the entire biosphere, although the intensity of effects will vary from place to place.

The three problems stemming from global atmospheric change--global climate change, increased ultraviolet-B radiation, and direct effects from increased carbon dioxide--share overlapping causes, have interacting effects and pose painful choices to decision-makers because they all involve significant uncertainties. A decade ago, the magnitude of the threat they posed concerned only a few scientists. It has since become clear that global atmospheric change ranks among the greatest threats to humankind, and that atmospheric changes themselves threaten biological diversity to a degree roughly comparable to physical habitat destruction.

To gain some idea of how these three trace-gas-induced kinds of atmospheric change are likely to affect biological diversity, it is useful to compare them in tabular form (Table 1).

Global climatic change will not be a simple warming of the planet. Even if it were, there would be major changes in the position and extent of the Earth's vegetation zones (Emanuel et al., 1985); for example, tundra would virtually disappear and the boreal coniferous forest (taiga) would shrink dramatically. Current predictions, however, indicate the warming will most likely not be simple and uniform. First, global circulation models have long predicted that warming will be greater over mid-continents than over windward coastal areas and at sea, and will be greater toward the poles than at lower latitudes. A more recent study (Stouffer et al., 1989) has produced the startling projection that warming in 2030 will be far greater in the Northern Hemisphere than in the Southern Hemisphere, and that some Southern Hemisphere areas could experience significant cooling.

Second, the actual patterns of warming will affect many other climatic phenomena. The world's climatic patterns, including rainfall, winds, hurricanes, tornadoes and thunderstorms with accompanying lightning (the cause of virtually all natural fires), are largely attributable to seasonal movements of airmasses in response to the movements of high and low pressure areas. The high and low pressure areas, in turn, are affected by the heat distribution on the Earth's surface. Much of the world's climate depends on relatively stable patterns of oceanic circulation. It is likely that these will not change gradually, but suddenly, as a reorganization of the planetary system of heat distribution (Broecker, 1989). As the distribution of ecosystems depends largely on the positions of airmasses (Neilson, 1987), any change in airmasses would have enormous impact on biological diversity. The ecological and social consequences of large, sudden changes would far exceed any resulting from predicted gradual warming.

Third, warming will have major consequences for the hydrological cycle. Unquestionably, warming will cause earlier snowmelt and a smaller proportion of precipitation falling as snow, which (unless there is higher rainfall) will mean lower streamflow in summer and fall, when human and biological demand for water is highest (Norse, 1990). Warming will increase evapotranspiration by plants, causing ecosystems to become drier unless there are large offsetting increases in rainfall. Warming will cause higher cloud cover over much of the planet and higher rainfall in some areas. However, general circulation models tend to predict that much of the increased rain is likely to fall over the sea, and some models predict that midcontinental areas will get less precipitation. So, some land areas will become wetter and some will become drier. The effects of increased dryness on the propagation of wildfires, a major determinant of many natural community patterns, and on outbreaks of disease organisms, merits special attention.

The threat of increased UV-B radiation caused by stratospheric ozone depletion is less certain. Although the course of increase in UV-B is much easier to predict than the course of climatic changes, the effects of such changes are much less certain. Studies of the effects of climate on the biota date back more than a century, while studies of UV-B are mostly very recent and incomplete. It is known that UV-B affects DNA synthesis, damages immune systems, increases skin cancers and causes cataracts in mammals. It is further known that UV-B disrupts marine planktonic communities (Worrest and Grant, 1989) and affects some tree seedlings (Sullivan and Teramura, 1988). The magnitude of these effects on populations, species and ecosystems is still hard to predict.

Unlike some other trace gases involved in global change, carbon dioxide has direct physiological effects on plants. At first glance, these effects appear beneficial. CO_2 is essential for photosynthesis and may limit plant growth; increasing its concentration increases growth rates in many plants, an effect called "CO_2 fertilization." CO_2 also benefits plants' water relations. Plants take in CO_2 through open stomata, which also allows water loss (transpiration). At higher CO_2 concentrations, plants can keep more stomata closed, and therefore lose less water. Thus, increasing atmospheric CO_2 diminishes drought stress.

Plants using the two different major pathways of carbon fixation differ in their response to increased CO_2 levels. "C_3" plants benefit more from enhanced CO_2 conditions than "C_4" plants (which constitute a small fraction of temperate species but a large fraction of tropical and desert species). Further, as Fajer (1989) notes, the magnitude of CO_2 growth enhancement in C_3 plants is species-specific. Thus, increasing CO_2 will alter competitive interactions between plant species. It is possible that many C_4 plants will become rarer or extinct and that there will be large changes in abundances of C_3 plants in the next century, which could have important consequences for food webs, community structure and ecosystem processes such as nitrogen fixation and soil formation. Species that we consider "weeds" could dramatically increase in abundance, stimulating increased efforts at control.

Additional complications could further affect biological diversity. CO_2 enrichment decreases the nitrogen content of plant tissues, prompting herbivorous insects to respond in several ways. Lincoln et al. (1984) found that tested larvae increased their feeding rates, indicating that "...the increased levels of plant productivity at higher CO_2 concentrations may be offset by higher herbivory and could even be reduced below current levels." Lincoln's more recent research on four other herbivorous insects and their hosts has consistently found increased feeding rates. But Fajer et al. (1989) found increased mortality in early larval instars of one species feeding on foliage grown under enhanced CO_2 conditions (and thus having decreased nitrogen content). This indicates that herbivorous insects could become less abundant, with effects including reduced abundances of insect-feeders.

5. Alien species

How does the addition of alien species affect biological diversity? Each case is different, but some generalizations can be made. It is clear that organisms evolve not only in response to their physical environment and to members of their own species, but in response to other species as well. This coevolution between hosts and parasites, predators and prey, and between mutualists means that the biological fabric of a community is distinctly interwoven; it is not just a random collection of threads. Species interact in myriad ways that we are only beginning to discover.

Alternatively, it is clear that communities generally have some "slack"; ecosystems are not so tightly organized that they cannot accommodate some compositional changes. Paleoecology shows that current assemblages of species did not exist in the recent geological past; some species that coexisted in the late Pleistocene are now allopatric (their ranges do not overlap) (Graham, 1986).

When a species is introduced into a new area, the alien species generally disappears. Sometimes, however, the alien species survives and proliferates in its new niche. This is particularly common in areas with "naive biotas" such as islands (e.g., Hawaii) (Vitousek, 1986) or areas that are now "undersaturated" as a result of previous climatic changes (e.g., southern Florida) (Courtenay, 1978). Not having evolved in these ecosystems, and thus being much less vulnerable to indigenous predators, parasites and competitors that have evolved no ways of dealing with them, alien species are sometimes able to proliferate to the point that they disrupt existing communities.

Rabbits (Oryctolagus cuniculus) introduced from Europe overwhelmed Australia; Australian Melaleuca thickets are overrunning Florida; white-tailed deer from the United States are wreaking havoc in New Zealand, and so on. Every organismic biologist can provide many examples of how introduced species have adversely affected native biotas, profoundly changing ecosystem dynamics and causing extinctions.

The problem is not limited to the land. As with many freshwater fish communities, those of the Great Lakes have been irrevocably changed by the introduction of alien species, in this case, predatory sea lampreys and planktivorous alewives (Alosa pseudoharengus). Although alien species in marine ecosystems have attracted much less attention, there is now excellent research showing their importance in undersaturated ecosystems such as Coos Bay, Oregon (for example see Carlton, 1989).

Introduction of aliens can be even more difficult to reverse than physical alteration or chemical pollution. At least in some cases, lands and waters can be restored to something resembling their original physicochemical conditions if dams are removed or pesticides are allowed to degrade. Alien species, however, can reproduce themselves; rats, cats and goats have thus far proved impossible to control, although there are prospects that introduced parasites could help (Dobson, 1988).

Compared with progress against chemical pollution, there has been little progress in dealing with the "biological pollution" of alien species. While it is too late to bring back many species-such as the Mariana fruit-dove, an endemic of Guam that was swallowed up by the introduced brown tree snake, it is possible to set priorities for controlling alien species (Westman, 1990) to slow the damage to native organisms.

6. Interactions

In 1894, a lighthouse keeper named Travers and his cat Tibbles moved onto Stephen Island, between New Zealand's North and South Islands (Fuller, 1987). Tibbles killed a small, brown, nearly flightless bird that had never been described by scientists, then another and another until the total was 16. Then there were no more. One cat had driven the Stephen Island wren (Xenicus lyalli) to extinction (Day, 1981). Seldom does the cause of extinction or ecosystem destruction appear so clear-cut. It is much more common for living things to be caught between two or more forces, none of which individually would be so destructive.

There is no lack of examples, but the situation in Hawaii is a classic. These islands, the most isolated in the world, were "a land of Eden" (Scott and Sincock, 1985). Polynesians, the first human colonists, arrived about 1500 years ago bringing rats, pigs, dogs, a love for bright colors manifested in the royal capes they fashioned from native songbird feathers, and agriculture, for which they cleared and burned the forests below 3300 feet. The naive island biota was devastated, with extinctions of at least 45 species of endemic birds, including a petrel, 2 ibises, 7 geese, a hawk, an eagle, 7 rails, 3 owls, 2 crows, a honeyeater and at least 15 honeycreepers.

The arrival of Europeans starting in the 1700s introduced new farming techniques and even more rapacious species of rats, as well as cats, mongooses, deer, sheep, cattle, snakes, 160 species of birds (of which about 50 have become established). For the native Hawaiian birds, perhaps most important of all was the introduction of bird malaria and its mosquito vectors. Together, this combination of predators, diseases, competitors and habitat destroyers shattered the Hawaiian flora and fauna, eliminating (again using the birds as an example) 2 more rails, 3 thrushes, 4 more honeyeaters and 9 more honeycreepers since the arrival of Europeans. The extinctions continue; 24 of the remaining 37 land bird species are endangered (Jehl, 1988).

This situation is not confined to islands. Continental biotas have long been subjected to similar combinations. They are inherently less vulnerable than long-isolated island biotas and have held out better, but pressures are steadily mounting.

Perhaps the greatest threat to biological diversity is the impending interaction between the stresses of climate change and habitat fragmentation. Alone, each is a major threat affecting a large percentage of species and ecosystems. Together, habitat fragmentation will reduce the ability of species to migrate in response to climate change. Man-made barriers to migration include roads, cities, agricultural land and static borders demarcating wildlife refuges. As Wilcox (1980) notes:

> The Pleistocene Epoch was marked by global temperature oscillations during which fairly extensive latitudinal (and altitudinal) shifts in climatic zones occurred. Normally, as climatic zones shift, so do the associated biotas. Insular regions, however, typically do not span a sufficient latitude to provide refugia for species ill-adapted to a novel climatic regime--and extinction results.

Peters and Darling (1985) took the threat of changing climate on biological diversity much farther, pointing out that even without human-imposed barriers to dispersal, bands of warmer climate moving poleward will advance at rates greatly exceeding the dispersal capabilities of many important species (e.g., trees). As a result, all but the fastest dispersers (many of which we call weeds and pests) will lose far more of their ranges at the equator-ward ends than they will gain at the pole-ward ends. Many species with small latitudinal ranges stand to lose their entire range.

Some species will find refuge at higher, cooler elevations, but here too there is risk of being trapped between forces (Norse, 1990). Area generally decreases with elevation, thus highlands will accommodate fewer species than lowlands currently do. Further consider the consequence of stratospheric ozone depletion; higher elevations already have higher UV-B levels, but depletion of the ozone layer will increase UV-B beyond what previous refugees in the mountains experienced.

Rather than being the exception, interacting environmental stressors as threats to biological diversity are the rule. Norman Myers (1987) summarized the importance of such interactions by noting:

> ... a one by one analysis of the discrete processes will surely underestimate the scope and scale of the eventual extinction.
>
> So the synergistic connection could well prove to be a major, if not the predominant, phenomenon at work during the extinction spasm impending.

Global amphibian populations may already be the victims of such unexplored interactions between stressors. Though not yet well documented, enough reports of unexplained amphibian population declines and local extinctions have circulated over the last several years that the National Research Council has decided to sponsor a panel of inquiry (Roy McDiarmid, personal communication).

E THE MAGNITUDE OF THE THREAT

1. Overview

The knowledge base is currently insufficient to assess the risks to biological diversity with quantitative rigor. Current estimates of the number of extant species on the earth vary by a factor of 10, a universally recognized system of classifying ecosystems has yet to be developed, and scientists lack knowledge of the amount of genetic diversity within the species of any region. Furthermore, scientists must investigate the factors that determine rates of key ecological processes such as soil formation, nitrogen fixation, and net primary production, and better understand threats to biodiversity, before any quantitatively accurate assessment can be made.

Nonetheless, it is possible to make very general observations. Table 2 plots major stressors versus major taxa, functional groups and ecosystems. This two-dimensional matrix could be useful in guiding actions within a limited geographic area and a limited timeperiod. This matrix could be improved at some future time by 1) accounting for geographic differences; 2) showing how stressors are changing over time; and 3) incorporating effects of interactive stressors on biota. For example, acid precipitation depresses nitrogen fixation, and the extent to which carbon dioxide directly affects plant growth depends on the availability of limiting substances, particularly soil nitrogen. Similarly, it matters little whether UV-B radiation affects great whales directly if it severely disrupts the composition and productivity of the zooplankton on which they depend.

Table 2 represents the best estimate of the author, Elliott Norse, with consideration given to the opinion of avian ecologist David Blockstein. In general, there was high concordance between the two views. To verify and build upon these data, a select group of ecologists could be surveyed at some future date.

Recognizing the limitations in scope and sources, Table 2 represents a prototype, containing the obvious threats to diversity within major taxonomic or functional groups and communities, within the next 50 years, in the contiguous United States. Specifically, Table 2 answers "To what degree will diversity be decreased by each of these stressors?" It is recognizing that, while diversity might decline, virtually all stressors benefit some species, communities and processes at the expense of others until the transcendence of some threshold beyond which even the hardiest organisms are harmed.

It is also important to know what measures are the best indicators of biological diversity and ecosystem integrity. Working on experimentally acidified lakes in Canada, Schindler and coauthors (1985) have shown that an ecosystem's species composition and measures of population health are valuable indicators of stress because the functional redundancy in ecosystems ensure that some raw ecosystem measures--such as primary production--can continue unaffected even in severely stressed ecosystems with dramatically changed species composition of primary producers and other organisms.

Certain shortcomings must be considered. This matrix is weighted heavily towards groups for which data are available or at least reasonable inferences are possible. For example, there are categories for several different nesting guilds of birds; birds are the best-studied organisms, and clear patterns have emerged about their vulnerability to some stressors. On the other hand, there are no categories for different groups of insects; undoubtedly flying insects and soil insects will differ in their response to many stressors. Bacteria were not included due to lack of information, despite the high importance of bacteria in any ecosystem (see Pimentel et al., 1980). The subdivision of biota is admittedly subjective and may stand improvement. Additionally, separate matrices for Alaska, Hawaii, American territories and other nations may prove similarly useful.

In the matrix, "excessive taking" refers to deliberate killing and removal of targeted organisms via hunting, trapping, animal damage control, fishing, and collecting, but not logging. "Incidental taking" refers to the unintended killing of non-target organisms because of the above activities. Thus, a Kemp's ridley sea turtle drowned in a shrimp trawl is a victim of incidental taking. "Physical alteration" is the most inclusive category, in that it includes simplification, fragmentation and destruction of ecosystems for timber, agriculture, minerals, housing, commercial and industrial development. It might be useful for this category to be broken down into several separate categories in future efforts to refine this methodology.

"Pesticides" refers to substances administered specifically to kill living organisms. "Industrial discharges" refers to discharge and dumping of any toxicants (including pesticides) into streams, rivers, lakes and the sea. "Fertilizers/sewage" includes the causes of eutrophication, mainly in aquatic systems. "Solid wastes" refers to nontoxic garbage. "Conventional air pollutants" include emissions of sulfur and nitrogen oxides, carbon monoxide, ozone and particulates. "CO_2" refers to anthropogenic carbon dioxide as a cause of direct physiological effects, not as a greenhouse gas. "Climatic change" refers to the suite of human activities that cause increases in greenhouse gases. "Alien species" refers to animals, plants and microorganisms introduced into natural ecosystems (not agriculture or ranching). "Nuclear wastes" refers to deliberate disposal of nuclear wastes. While this list of stressors is certainly not all inclusive, most major stressors are represented.[2]

Each interaction between taxonomic grouping and stressor is rated with one of four symbols. An open circle denotes a negligible or minor impact. A half-filled circle is a substantial impact that merits study and quite possibly remedial action. A filled circle is a very serious threat that deserves immediate priority for study and action. A question

[2] Two exceptions should be noted. First, the unintentional killing of organisms due to activities unrelated to intentional taking or the other listed categories is not considered, but is significant in some cases (e.g. manatees hit by boats or turtles run over by cars). Updates of this report should include such "accidental killing" under "incidental taking." Second, it is unclear whether accidental spills of hazardous substances (e.g. oil spills) are included in the assessment of risk from "industrial discharges." This should be clarified in any update.

mark indicates that there is not enough information to make a reasonable judgment, or that the available information leads to conflicting conclusions. A question mark in addition to a symbol indicates the rating is less certain.

2. Status of the best-known taxon: Birds[3]

Taxonomic groups of living organisms differ so greatly that none is truly representative of all groups. Still, better data exists for some groups and can provide limited indications for application to other taxa. Birds have been studied more extensively than any other group, due in part to their colorful and conspicuous nature. Virtually all bird species have now been scientifically described, and many thousands of scientists and birdwatchers observe them in both developed and developing countries. Despite their importance in ecosystem functioning, the same cannot be said of plants, fungi, fishes or mites.

Data on bird populations in the United States are maintained by the Fish and Wildlife Service (FWS). Certain species (such as waterfowl) have been systematically monitored; songbird populations have been assessed since 1965 in the FWS-coordinated breeding bird surveys; and wintering populations have been counted since 1900 in the National Audubon Society Christmas bird census. Despite these efforts, there is no central repository of population data, the quality of the data are highly variable, and the taxonomic distribution of data collection is uneven. Documenting general trends is extremely difficult and nothing better than educated guesses are available for many groups of species (Jehl, 1986). Jehl's chapter in the Council on Environmental Quality's 1986 Annual Report summarizes status and trends of the birdlife of the United States. International data have been more generally summarized for rare birds by the International Council for Bird Preservation.

The following summary presents information on major groups of birds, first in the United States, and second, internationally. As Jehl noted, some 70% of the 1000-1350 bird species occurring in the United States spend at least part of their annual cycle outside the United States (Jehl, 1986). His paper is the basic reference for all data not otherwise attributed.

a) Seabirds. The total seabird population in North America and adjacent oceans approximates some 100 million birds of 106 breeding species. Tens of millions of southern hemisphere breeders spend time north of the Equator. While population status is unknown for at least 75% of these species, some trends are apparent. Scavenging commensals of humans (gulls and fulmars) are thriving. Terns are declining, due to competition with gulls and with humans for nesting habitat. Some fish-eaters (pelicans and cormorants) are showing recovery from pesticide-induced declines. In general, North American seabirds appear to have been stable or increasing over the past few decades. Greatest threats are to temperate and tropical nesters whose habitats are being lost to disturbance by humans, including development on beaches where the birds nest.

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[3]This section was primarily written by avian ecologist David E. Blockstein.

Other threats include entanglement in drift nets and ingestion of plastic and other debris. Entanglement rates are high, but may not reduce overall populations. Local impacts are very significant, however, in areas with much driftnet fishing (such as the North Pacific) and in the North Atlantic, where entanglement occurs with conventional nets. Ingestion of large amounts of plastic has been documented in many species of seabirds. Present rates and amounts of ingested plastic are too small to have effects on most species. Certain populations that have been well studied, such as albatrosses in Hawaii, show chick mortality due to plastics.

b) Waterfowl. Data on waterfowl are as good as on any group. The FWS has documented a continuing overall decline in duck populations in North America since monitoring began in 1955. Populations are presently at their lowest level since that time. Populations of mid-continental breeders, which include more than 50% of North American waterfowl, are in critical declines. This is largely due to habitat destruction of wetland breeding areas, such as marshes and potholes, to accommodate agriculture. The recent drought has exacerbated this situation to the point where hunting has been restricted. A 15-year multi-million dollar North American Waterfowl Management Plan has been approved by Congress to purchase breeding and wintering habitat.

Populations of geese, which generally nest in the tundra, are mostly stable. The exception are geese who nest in western Alaska, where overhunting by sport and native subsistence hunters is depleting populations. Loons have decreased throughout the century, largely due to disturbance on their northern nesting grounds. Some range expansion has occurred recently. However, acid rain and interactions with mercury pollution may have significant effects that are just being investigated in these fish-eaters.

c) Colonial wading birds. The 16 U.S. species of wading birds are highly dependent on wetlands. Recently, some good monitoring has been done by ornithologists from FWS and other groups. By the 1970s, ranges had been recovered from feather trade depletions of 1880-1900, which nearly eliminated many species (and led to the formation of the National Audubon Society). Total numbers are still reduced. Overall most populations have remained relatively stable, except wood storks, which are now endangered, and cattle egrets, which are self-introduced from Africa and are increasing exponentially. Local declines are most serious in California and southern Florida, where there has been almost total collapse of a wading population that once numbered in the hundreds of thousands (Ogden, 1987). Habitat loss due to wetland conversion is a key stressor as are harmful water management practices. Pesticides and irrigation practices have had significant local impacts.

Unless wetland conversion is reversed, significant declines are expected in this group.

d) Raptors. Six of the 50 raptor species breeding in the United States are endangered. Most populations have increased from historic lows caused by shooting, human disturbance and development, and DDT and other pesticides. Despite recovery, they generally remain below historic levels. Bald eagles and peregrine falcons have recovered substantially due to heavy manipulative rescue efforts. Some species (e.g. harriers, Swainson's hawks, and red-shouldered hawks) are declining due to habitat loss.

Population data rarely exist for owls, but the northern spotted owl is an exception. The habitat of the northern spotted owl has been systematically and rapidly reduced by the unsustainable logging practices of the U.S. Forest Service to the point where it is now proposed for listing as a federally threatened species. Logging plans for the old-growth forests of the Pacific Northwest mark the first time that a conscious decision has been made to reduce a non-pest species to a critical population level (Dawson et al, 1987). The southern spotted owl may soon reach the same status.

Raptors are excellent indicators of environmental health due to their susceptibility to disturbance and chemicals, and due to their low rate of recovery. Overall signs are positive, but specific cases could be regarded as warnings.

e) Gamebirds. Few reliable data exist for the 28 species of non-migratory game birds. Wild turkey and ruffed grouse have increased due to restoration programs. Prairie-nesting grouse are generally in decline due to habitat conversion for agriculture.

Mourning doves are extremely abundant and well-monitored. They have increased in the north central states and prairie provinces as a result of increased agriculture (doves instead of ducks), but are declining in the West, perhaps due to a combination of land conversion (development) and overhunting. The overall population is declining, according to FWS call count surveys.

f) Shorebirds. Some 49 species of shorebirds breed in North America. Extensive hunting virtually eliminated populations of many species by 1927, when most hunting was closed. Only the Eskimo curlew remains endangered. Data for 12 Atlantic coast migrants show significant declines for 3 species and no detectable trends of the others, but the data are of variable quality.

Populations of piping and snowy plovers, which nest on sandy beaches, are severely declining; some populations of piping plovers have been listed as threatened. Grassland nesters are also undergoing population decline.

Migratory shorebirds are extremely vulnerable because they concentrate on a relatively small number of traditional stopover sites (some 50 in North America). These are likely to be irreplaceable. Destruction of key sites due to development, oil spills or other environmental change could be disastrous to many shorebird species. The National Audubon Society has organized a voluntary effort to establish a Western Hemisphere Shorebird Reserve System.

Shorebirds are also vulnerable to habitat destruction, pesticide poisoning and pollution of their wintering grounds on the beaches of the Americas. Only recently has a major effort begun to color-band individuals in order to discover which breeding populations use which migration and wintering sites.

Most shorebirds breed in the Arctic tundra. Thus, they and other tundra groundnesters (geese and songbirds) are extremely vulnerable to global warming. If projections that warming will be most severe at the polar regions are realized, shorebirds will suffer critical declines because their nesting areas will be flooded.

g) Songbirds. Approximately 50% of the North American avian species are small landbirds. Most nest in woodlands and a smaller percentage nest in fields and grasslands. Population trends come from breeding bird surveys (BBS) since 1965 and a few long-term or multi-site studies of forest-dwelling birds. Most of these birds are migratory, many (especially forest-interior songbirds) wintering in the neotropics.

Grassland birds are generally declining. This is especially true in the East where farms and pastures revert to secondary forest. As much of the East was once forested, these declines may represent a return towards pre-settlement conditions. Riparian breeders are of special concern in the West, especially in California, due to habitat destruction and loss of streamflow to irrigation.

A major summary of population declines in migratory birds in eastern North America has just been published (Askins et al., 1990). It summarizes data showing severe and catastrophic declines in some species of forest birds in the United States since monitoring began in the 1940's and 1950's. Most of these declines are of neotropical migrants inhabiting forest interiors.

Long-term studies in small urban and suburban forest preserves show declines in interior species, but not in more resident edge-dwelling species. These changes may be due to local impacts related to forest fragmentation and the edge effect or to destruction of wintering habitat.

Data are inconsistent in the few long-term studies of extensive (>1000 ha) forest tracts. Declines in migrants, where they occurred, have not been as severe as in small forests. Some changes may be related to habitat change as the forests mature.

Many neotropical migrants have lower densities in small forests than in large forests and some species tend to be absent from small forests. Experimental and observational evidence show that open-cup nesting species (most neotropical migrants) have low reproduction in forest patches due to nest predation by edge-living species and brood parasitism by brown-headed cowbirds (also an edge species).

In tropical wintering areas, many species of forest-dwelling migrants have much higher densities in secondary and mature forests than in early successional stages. Most migrants winter in the Caribbean basin, where deforestation trends foretell major population declines.

Breeding Bird Survey data show that most neotropical migrants have declined during the past 11 years following a period of stable or increasing populations during the late 1960s and '70s. Absolute declines and declines in rate of population increase are almost restricted to species that are concentrated in forests during the winter, even those that nest in early successional habitats during the summer. This may constitute the first unambiguous evidence of declines in populations of neotropical migrants due to the destruction of winter habitats (data analysis by Russ Greenberg).

Thus, declines in populations of forest-dwelling songbirds are due to habitat fragmentation on the breeding grounds and habitat destruction on the wintering grounds: The old double whammy. These birds are in serious trouble unless present trends are reversed.

There has been little quantitative study of forest birds in the West.

h) Island birds. An estimated 93% of all species and subspecies of birds that have become extinct since 1600 were island natives (King, 1978).

Hawaii: The Hawaiian Islands boast the highest percentage of endemic flora and fauna in the world. Before the Polynesians arrived, there were some 94 species of endemic land birds. Half of these were subsequently exterminated due to destruction of lowland forests, and predation and habitat destruction by dogs, rats and pigs. Thirteen additional species have gone extinct since the arrival of Europeans in 1778. Today, only 37 species of native land birds remain. Some 24 of these (65%) are endangered, all but 3 of which are endemic; six species number fewer than 50 individuals.

The future for remaining native species of Hawaii appears bleak, as the stresses to biological diversity continue unabated. Deforestation for logging and development, habitat disturbance by feral and alien mammals, introduction of alien birds and plants, and spread of avian diseases (many of which are transmitted by introduced mosquitoes) all continue. The problem of disease prevents many species from occupying otherwise suitable lowland forests. Some species of seabirds and waterbirds are also at risk due to habitat destruction and disturbance by introduced species.

Guam: Originally there were 18 species of birds on Guam, 12 of which were landbirds. Since the inadvertent introduction of the Solomon Island brown tree snake in the 1940s or '50s, the spread of this bird- and lizard-eating snake has paralleled the decline of forest-dwelling birds. As of 1987, 7 species or subspecies of landbirds were extinct and 4 more were on the verge of extinction, with populations numbering less than 100 individuals. Micronesian kingfishers and Guam rails have been removed and are thriving in captive breeding programs. The rails will be reintroduced as an experiment on the small nearby island of Rota.

The case of the extermination of an entire avifauna by a snake is unique. The contribution of other factors such as deforestation have not been assessed. One of the few remaining large tracts of forest is slated for destruction by the Navy in order to build a satellite tracking station. This area would be a site for reintroduction if the snake can be controlled. Plans are presently under review by the FWS. The brown tree snake and other species have been discovered on other Pacific islands (including Hawaii) as a result of inadvertent transport with cargo. Whether the history of Guam will be repeated elsewhere may depend upon local conditions.

i) International. There are about 9000 species of birds in the world. According to the International Council for Bird Preservation, 1029 species (11% of all species) are, to varying degrees, at risk of global extinction. This only includes birds whose status is known. Potentially threatened species might increase the number 3- or 4-fold. A truer picture might be obtained by listing species that are "safe". Such information, however, is not available.

Basically, birds are threatened in every taxonomic group and in every geographic area. Most critical are islands, but habitat islands caused by fragmentation of forest and other continuous habitats are likely to also have high rates of extinction.

Some 1500-2000 species of birds depend on lowland tropical forests. The destruction of these biologically diverse habitats will result in tremendous extinction of birds as well as other species.

Habitat destruction is clearly the leading threat to bird species. A major, but uncounted toll is probably taken by pesticides, which are still heavily used in much of the developing world. Pollution of air and water may be an important factor in some areas. Direct exploitation for food significantly affects some species, particularly large birds such as guans and galliformes, and colonial nesting seabirds and waterbirds. Millions of migrating songbirds and raptors are netted and shot as they cross the Mediterranean. Competition from alien species is significant in some cases, particularly on islands. Global warming would have its greatest impact on species that breed in Arctic and coastal habitats. Shorebirds are especially vulnerable from both of these threats.

Despite the fact that birds can fly and are often envisioned as mobile enough to escape unsuitable conditions, many species are running out of places to go to. The future of the birds of the world looks no brighter than of other taxa.

IV Conclusion

The biological diversity crisis presents the human race with a painful dilemma. It is clear to many people that something momentous is happening to the global environment and that it cannot be let go too far lest indispensable resources and life support systems be lost. It is equally clear that acting to remedy the situation will have substantial costs, and that great uncertainty exists. Lack of information and short-term economic costs, however, cannot be valid excuses for inaction. Rather, they place a premium on gathering intelligent, insightful analysis of whatever information is at hand and using the best possible theory and intuition, so that the best possible choices can be made.

Homo sapiens must learn to coexist with wildlife, or learn to live in a world with fewer options and much less variety. Decisions to preserve and restore land for the direct benefit of wildlife, and the indirect benefit of humans, must be made now or the opportunity will be lost.

V TABLES

Table 1. Three kinds of global atmospheric change affecting biological diversity.

	Global climate	Increased UV-B	Increased CO_2
Causes	Fossil fuels Land use Manufacturing	Manufacturing	Fossil fuels Land use
Trace gases	CO2, CFCs, Methane, Nitrous oxide	CFCs, Halons, Light chlorinated hydrocarbons	CO_2
Understanding of physical effects	Low	Medium	High
Understanding of biological effects	Medium	Low	Low
Likely impact on biodiversity in 50 years	High	Medium	Medium
Likely impact on biodiversity in 100 years	Very high	Medium	High

Table 2: Overview of Threats to Biological Diversity in the Contiguous 48 States

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○ Minor impact
⊘ Substantial impact
● Very serious threat
? Lack of or conflicting information

	Intentional Taking	Incidental Taking	Physical Alteration	Pesticides	Industrial Discharges	Fertilizers/ Sewage	Solid Wastes	Air Pollutants	CO_2	UV-B	Climatic Change	Alien Species	Nuclear Wastes
TERRESTRIALS													
Mammals													
Large	⊘	○	●	○	○	○	○	○	○	⊘	●	○	○
Arborial	○	○	⊘	○	○	○	○	○	○	⊘	●	○	○
Small	○	○	⊘	○	○	○	○	○	⊘	⊘	●	○	○
Bats	○	○	●	●	○	○	○	⊘ ?	⊘	○	⊘	○	○
Birds													
Hole-nest	○	○	●	⊘	⊘	○	○	○	⊘	○	⊘	⊘	○
Canopy-nest	○	○	⊘	⊘	⊘	○	○	⊘ ?	⊘	⊘	⊘	○	○
Ground-nest	○	○	●	⊘	○	○	○	⊘ ?	⊘	⊘	●	○	○
Reptiles	⊘	○	⊘	⊘ ?	○	○	○	○ ?	⊘	○	●	○	○
Amphibians	○	○	●	⊘ ?	●	⊘	○	●	⊘	⊘	●	○	○
Arthropods	○	○	⊘	⊘	○	○	○	○ ?	⊘	○	⊘	○	○
Snails	○	○	●	○ ?	○	○	○	⊘ ?	⊘?	○?	●	○	○
Conifers	○	○	●	○	○	○	○	●	⊘	⊘	●	●	○
Brdlf Tree	○	○	⊘	⊘	○	○	○	⊘ ?	⊘	⊘	●	●	○
Herbs	⊘	○	●	⊘	○	○	○	⊘ ?	⊘	⊘	●	⊘ ?	○
Fungi	○	○	⊘	○ ?	○	○	○	●	○	⊘?	⊘	○	○
Shrublands	○	○	⊘	○	○	○	○	⊘	⊘	⊘?	⊘	⊘	○
Grasslands	○	○	●	⊘	○	○	○	○	⊘	⊘?	⊘	●	○
Tundra	○	○	⊘	○	○	○	○	⊘	⊘	⊘?	●	○	○
Deserts	○	○	⊘	○	○	○	○	○	●	○	⊘	⊘	○

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	Intentional Taking	Incidental Taking	Physical Alteration	Pesticides	Industrial Discharges	Fertilizers/ Sewage	Solid Wastes	Air Pollutants	CO_2	UV-B	Climatic Change	Alien Species	Nuclear Wastes
FRESHWATER													
Stream													
Amphibians	○	○	●	⊘ ?	⊘	⊘	○	●	○	⊘?	●	○	○
Fishes	○	○	●	⊘	⊘	⊘	○	●	○	○	●	⊘	○
Insects	○	○	●	●	⊘	⊘	○	●	○	○	⊘	⊘	○
Producers	○	○	⊘	⊘ ?	⊘	●	○	●	○	○	⊘	○	○
River													
Birds	⊘	○	⊘	⊘	⊘	⊘	○	○	○	⊘?	⊘	○	○
Reptiles	○	○	⊘	○	○	○	⊘	○	○	○	⊘	○	○
Amphibians	○	○	⊘	⊘ ?	⊘	⊘	○	○	○	○	●	○	○
Fishes	○	○	●	⊘	●	⊘	○	○	○	○	●	○	○
Molluscs	⊘	○	●	○ ?	●	⊘	○	○	○	○	●	○	○
Insects	○	○	⊘ ?	⊘ ?	⊘	●	○	○	○	○	⊘	○	○
Emerg Plants	○	○	⊘	⊘ ?	⊘	⊘	○	○	⊘	⊘?	●	○	○
Algae/SAV	○	○	⊘	⊘ ?	●	●	○	○	○	○	⊘	○	○
Lake/Wetland													
Birds	⊘	○	⊘	⊘	⊘	○	○	⊘	○	⊘?	⊘	○	○
Amphibians	○	○	⊘ ?	⊘ ?	⊘	⊘	○	●	○	○	●	○	○
Fishes	○	○	⊘	⊘ ?	●	●	○	●	○	○	●	●	○
Molluscs	○	○	⊘ ?	⊘ ?	⊘	⊘	○	⊘	○	○	●	○	○
Insects	○	○	⊘ ?	⊘ ?	●	⊘	○	⊘	○	○	⊘	○	○
Emerg Veg	○	○	⊘	⊘ ?	⊘	○	○	○ ?	●	⊘?	⊘	○	○
Algae/SAV	○	○	⊘ ?	⊘ ?	●	●	○	⊘ ?	○	○	⊘	○	○
Cave Dwellers	⊘	○	⊘	⊘ ?	⊘	○	○	⊘ ?	○	○	⊘	○	○

Table 2: Overview of Threats to Biological Diversity in The Contiguous 48 States

○ Minor impact
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? Lack of or conflicting information

	Intentional Taking	Incidental Taking	Physical Alteration	Pesticides	Industrial Discharges	Fertilizers/ Sewage	Solid Wastes	Air Pollutants	CO_2	UV-B	Climatic Change	Alien Species	Nuclear Wastes
MARINE													
Estu/Intr Tidal													
Birds	○	○	⊘	⊘	⊘	○	⊘	⊘	○	⊘	⊘	○	○
Fishes	⊘	○	○	○	⊘	●	○	○	○	○	⊘	○	○
Inverts	⊘	○	⊘	○	⊘	●	○	⊘	○	⊘	⊘	⊘	○
Dune Veg	○	○	●	○	○	○	○	⊘ ?	⊘	○	⊘	○	○
Mangroves	○	○	●	○	⊘	⊘	○	○	○	○	○	○	○
Seagrasses	○	○	●	○	⊘	⊘	○	⊘ ?	○	⊘ ?	○	○	○
Algae	○	○	○	○	⊘	●	○	⊘ ?	○	⊘ ?	⊘	⊘	○
Nearshore													
Mammals	○	⊘	○	⊘ ?	⊘	○	●	○	○	⊘	⊘	○	○
Birds	○	⊘	⊘	⊘ ?	○	○	●	⊘ ?	○	⊘	⊘	○	○
Reptiles	○	●	⊘	⊘ ?	○	○	●	○	○	⊘ ?	○	○	○
Fishes	⊘	⊘	○	○	⊘	⊘	⊘ ?	○	○	○	⊘	○	○
Plankton	○	○	○	○	⊘	⊘	○	○	○	●	⊘	○	○
Bnth Inverts	⊘	⊘ ?	⊘	○	⊘	⊘	○	○	○	○	⊘	○	○
Seagrasses	○	○	⊘	⊘ ?	⊘	●	○	○	○	⊘	⊘	○	○
Coral Reefs	⊘	⊘	⊘	○	⊘	●	○	○	○	○	○	○	○
Offshore													
Mammals	○	●	○	○	○	○	●	○	○	○	○	○	○
Birds	○	●	○	○	○	○	●	○	○	⊘	○	○	○
Fishes	⊘	⊘	○	○	○	○	○	○	○	○	○	○	○
Plankton	○	○	○	○	○	○	○	○	○	●	○	○	○
Benthos	○	○	○	○	⊘	○	○	○	○	○	○	○	⊘

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