

3

Threats to Biodiversity

Martha J. Groom

Extinction is the most irreversible and tragic of all environmental calamities. With each plant and animal species that disappears, a precious part of creation is callously erased.

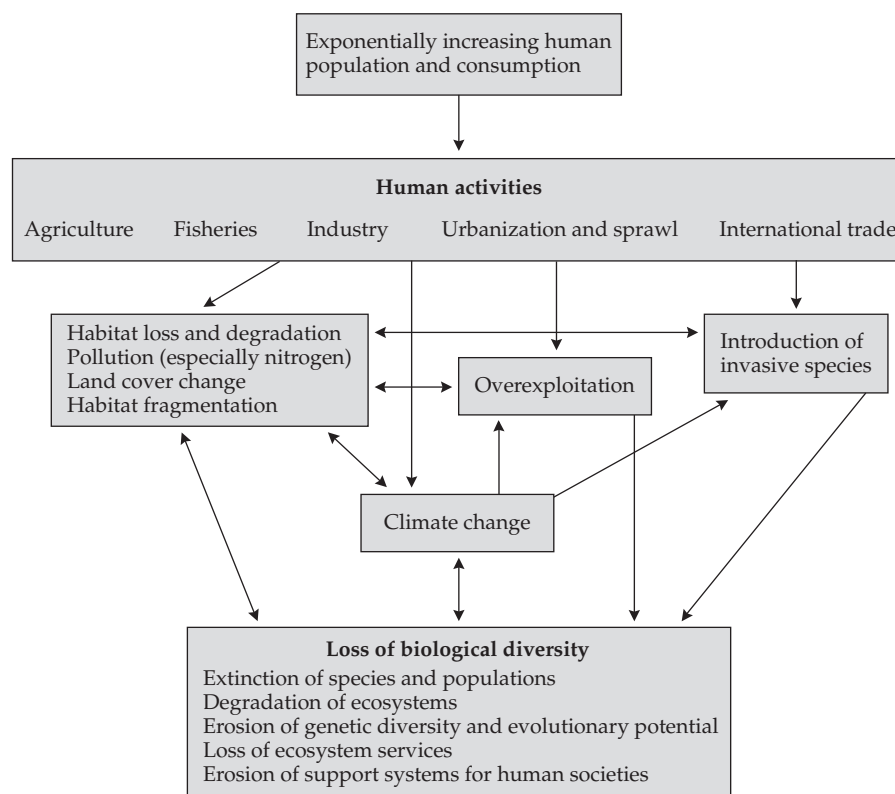
Michael Soulé, 2004

Human impacts are now a pervasive facet of life on Earth. All realms—terrestrial, marine, and freshwater—bear our imprint; our pollution spans the globe, our fisheries extend throughout the world's oceans, and our feet tread across almost every surface on Earth. By many estimates, we use substantial and increasing fractions of Earth's primary productivity (Vitousek et al. 1986; Pauly and Christensen 1995; Postel et al. 1996), and our total ecological impact may already extend beyond Earth's capacity to provide resources and absorb our wastes (Wackernagel and Rees 1996).

As humans became a widespread and numerous species, our agricultural expansion forever changed vast landscapes; our hunting and our transport of invasive, commensal species drove numerous aquatic and terrestrial species extinct. When highly organized societies began to settle and grow throughout the globe, the pace of transformation of terrestrial and aquatic habitats sharply increased, and our use of natural resources began to dramatically outstrip natural rates of replacement. Thus, humans have had enormous impacts on the form and diversity of ecosystems. Ultimately, we have set in motion the sixth great mass extinction event in the history of the Earth—and the only one caused by a living species.

Human population and consumption pressures are the root threat to biodiversity (see Chapter 1; Figure 3.1). Increasing numbers of humans, and most importantly, increasing levels of consumption by humans create the conditions that endanger the existence of many species and ecosystems: habitat degradation and loss, habitat fragmentation, overexploitation, spread of invasive species, pollution, and global climate change. Species extinction, endangerment, and ecosystem degradation are not the aims of human societies, but are the unfortunate by-product of human activities. Because our practices are unsustainable, we strongly erode the natural capital that we have used to flourish, thus endangering our and our descendants' future.

Figure 3.1 Major forces that threaten biological diversity. All arise from increases in human population and consumption levels, often mediated through our activities on the land and sea. Extinction and severe ecosystem degradation generally result from multiple impacts and from synergistic interactions among these threats.



Major Threats to Biodiversity and Their Interaction

In this chapter, I provide an overview of patterns of extinction and species endangerment, and describe efforts employed to slow and reverse these trends. The first step is to review the major types of threats to biodiversity, while laying the groundwork for the more in-depth coverage of these topics later in the book.

Habitat degradation includes the spectrum of total conversion from a usable to an unusable habitat type (or “habitat loss”), severe degradation and pollution that makes a habitat more dangerous or difficult for an organism to live in, and fragmentation that can reduce population viability. Habitat degradation can be caused by a host of human activities including industry, agriculture, forestry, aquaculture, fishing, mining, sediment and groundwater extraction, infrastructure development, and habitat modification as a result of species introductions, changes in native species abundance, or changes in fire or other natural disturbance regimes. In addition, most forms of pollution affect biodiversity via their degradation of ecosystems. Chapter 6 contains a full discussion of the impacts of various forms of habitat loss and degradation, while the phenomenon and effects of habitat fragmentation are detailed in Chapter 7.

Overexploitation, including hunting, collecting, fisheries and fisheries by-catch, and the impacts of trade in species and species’ parts, constitutes a major threat to biodiversity. Most obviously, a direct impact of overexploitation is the global or local extinction of species or populations. Less obvious, the decrease in population sizes with exploitation can lead to a cascade of effects that may alter the composition and functionality of entire ecosystems (Estes et al. 1989; Redford 1992; Pauly et al. 1998). Overexploitation is discussed in detail in Chapter 8.

The spread of **invasive species**, species that invade or are introduced to an area or habitat where they do not naturally occur, is also a significant threat to biodiversity. Invasive species can compromise native species through direct interactions (e.g., predation, parasitism, disease, competition, or hybridization), and also through indirect paths (e.g., disruption of mutualisms, changing abundances or dynamics of native species, or modifying habitat to reduce habitat quality). The process and impacts of species invasions are described in detail in Chapter 9.

Anthropogenic climate change is perhaps the most ominous threat to biodiversity of the present era. Climate change appears to have caused mass extinctions seen in the geologic record, and because the pace of climate change is predicted to be at least as fast and extreme as the most severe shifts in climate in the geologic

record, the effect on biodiversity is expected to be enormous. Coupled with the extensive transformation of Earth's ecosystems, widespread overexploitation of populations, and introductions of species to new areas in the globe, we can expect the effects of future shifts in climate to usher in an extremely severe mass extinction event. The probable biological impacts of the climate changes underway today are examined in full in Chapter 10.

As we are becoming more aware of the global impacts of climate change, we also are learning more about the global extent of pollution. We now recognize that in addition to direct discharge of chemicals into the environment, many are circulated atmospherically. Toxic compounds, such as lead, mercury, and other heavy metals, are found in trace amounts even in remote areas of Antarctica and the Arctic (Bargagli 2000; Clarke and Harris 2003), and are transported from industrial sources through the atmosphere. Importantly, many compounds can have subtle yet profound impacts on the endocrine systems of wild animals (see Chapter 6). Since the 1960s we have been aware of the dangerous consequences from many noxious chemicals, particularly those that **bioaccumulate** or magnify in

the food chain (Figure 3.2). In Essay 3.1, Peter Ross describes potential impacts of one particularly noxious class of pollutants—persistent organic pollutants (POPs)—on killer whales (*Orcinus orca*). POPs include the infamous DDT, which caused the decline of many raptor populations via eggshell thinning.

Diseases are also becoming more widespread, and our recognition of their impacts is increasing. Among the most noticeable and worrisome are outbreaks of disease that decimate coral reefs; as corals die, the complex community of fishes, algae, and invertebrate species is compromised (Harvell et al. 1999). Andy Dobson describes several examples of how diseases threaten populations and indirectly play an enormous role in altering ecosystems (Essay 3.2). Often, diseases become more dangerous as a result of interactions with the stresses caused by pollutants.

Typically, species and ecosystems face multiple threats. Importantly, the joint effects of several threats may be the ultimate cause of biodiversity losses. For example, the Dodo (*Raphus cucullatus*) went extinct on Mauritius in 1681 due to human overexploitation com-

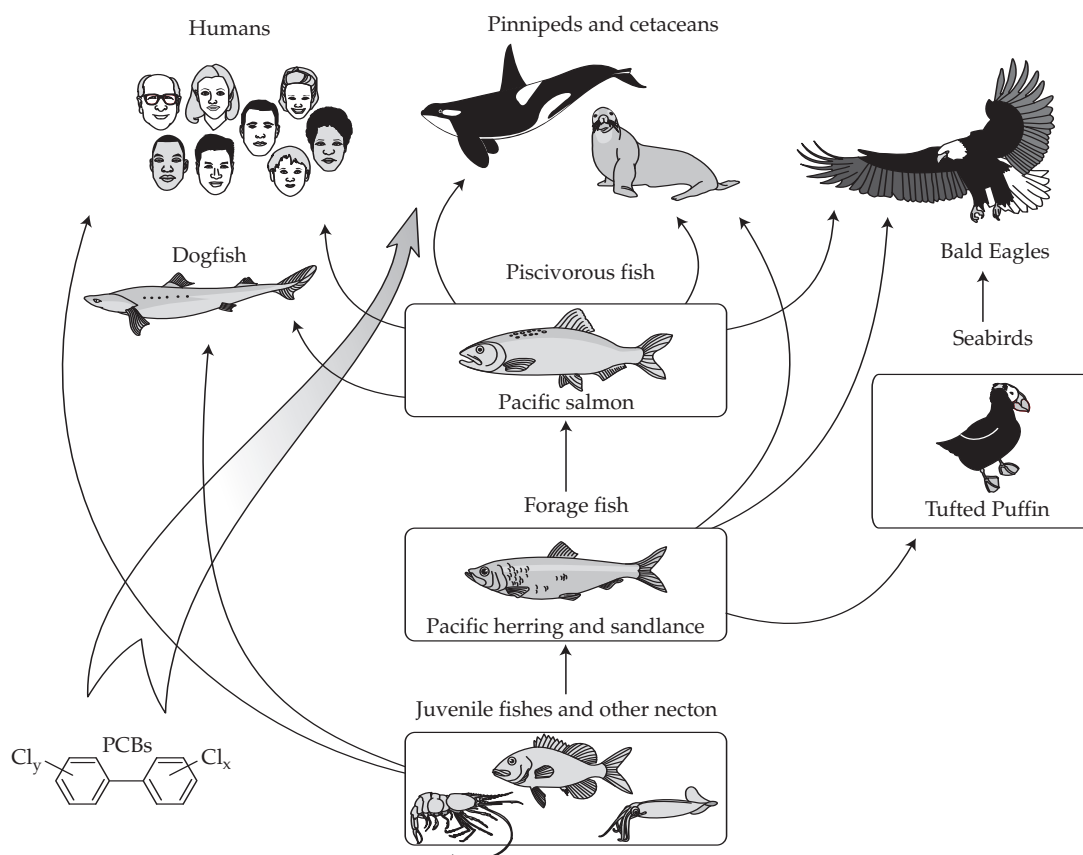


Figure 3.2 Toxic chemicals that accumulate in fatty tissues, such as PCBs and dioxins, concentrate in the tissues of organisms at the top of the food chain. (Modified from Ross and Birnham 2003.)

ESSAY 3.1

Killer Whales as Sentinels of Global Pollution

Peter S. Ross, *Institute of Ocean Sciences, Canada*

■ Persistent organic pollutants (POPs) comprise a large number of industrial and agricultural chemicals and by-products. While these chemicals have widely varying applications, they share three key features: They are *persistent*, *bioaccumulative*, and *toxic* (PBT). The physico-chemical characteristics of these chemicals dictate the degree to which they break down in the environment (persistence), the degree to which they are metabolically broken down or to which they accumulate in organisms (bioaccumulative potential), and the degree to which they bind to certain cellular receptors or mimic natural (endogenous) hormones in vertebrates (toxicity).

Marine mammals are often considered vulnerable to the accumulation of high concentrations of POPs as a result of their high position in aquatic food chains, their long life spans, and their relative inability to eliminate these contaminants. Because POPs are oily (lipophilic), they are easily incorporated into organic matter and the fatty cell membranes of bacteria, phytoplankton, and invertebrates at the bottom of the food chain. As these components are grazed upon by small fishes and other organisms at low trophic levels, both the lipids and the POPs are consumed. In turn, these small fishes are consumed by larger fishes, seabirds, and marine mammals that occupy higher positions in aquatic food chains. However, lipids are burned off at each trophic level and are utilized for maintenance, growth, and development, while the POPs are left largely intact. This leads to biomagnification, with increasing concentrations of POPs found at each trophic level. In this way, fish-eating mammals and birds are often exposed to high levels of POPs, even in remote parts of the world.

The killer whale (*Orcinus orca*) is one of the most widely distributed mammals on the planet. Although elusive and poorly studied in many parts of the world, these large dolphins have been the subject of ongoing study in the coastal waters of British Columbia, Canada, and Washington State. A long-standing photo-identification catalogue based on unique markings has facilitated the study of populations in this

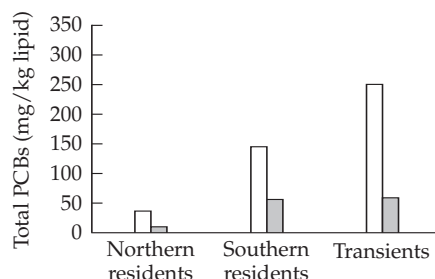


Figure A Transient killer whales represent the most PCB-contaminated marine mammal on the planet, reflecting their high trophic level (they consume marine mammals), long life span, and relative inability to eliminate these contaminants from their bodies. Females (in gray) are less contaminated than males (in white) because they transfer these contaminants to their offspring via fat-rich milk. (Modified from Ross et al. 2000.)

region (Ford et al. 2000). Several communities, or ecotypes, frequent these coastal waters, including the salmon-eating resident killer whales, the marine mammal-eating transient killer whales, and the poorly characterized offshore killer whales. There are two communities of resident killer whales: the northern residents that ply the waters of northern British Columbia, and the southern residents that straddle the international boundary between British Columbia and Washington. Our discovery that killer whales are among the most contaminated marine mammals in the world highlights concerns about the way in which POPs move great distances around the planet with relative ease (Ross et al. 2000; Figure A).

Studying marine mammal toxicology is not easy. Because deceased individuals are not generally considered representative of the free-ranging population, biopsy samplings of blubber from live individuals have increasingly been used to generate high-quality information about contaminant levels in their tissues. However, the resulting data are meaningless if nothing is known about the individual from which the biopsy sample originates. Age, sex, condition, and dietary preferences all represent important “confounding” or “natural” factors that affect the concentration of contaminants in the animal’s tissue. In

the case of killer whales, the photo-identification catalogue provides such a backdrop, with each sample originating from an individual of known age, sex, and community (hence dietary preference). Consequently, we were able to document that males became increasingly contaminated as they aged, while females became less contaminated as they transferred the majority of their contaminant burden to their nursing calves via fat-rich milk.

Many POPs, including the polychlorinated biphenyls or PCBs and the pesticide DDT, are highly toxic. Laboratory animal studies have conclusively demonstrated that such chemicals are endocrine disrupting, with effects noted on reproduction, the immune system, and normal growth and development. Studies of wildlife are more challenging, as free-ranging populations are exposed to thousands of different chemicals, and a number of other natural factors can affect their health. Captive-feeding studies have demonstrated that herring from the contaminated Baltic Sea affect the immune and endocrine systems of harbor seals (Ross et al. 1996). Studies of wild populations provide clues about the impact of POPs on marine mammals. However, as is the case with humans, a combined “weight of evidence” from numerous lines of experimental and observational evidence in different species provides the most robust assessment of health risks in animals such as killer whales (Ross 2000). This weight of evidence is based on inter-species extrapolation, and depends upon the conserved nature of many organ, endocrine, and immunological systems among vertebrates.

While regulations have resulted in many improvements for certain POPs, new chemicals are designed each year. Killer whales represent a warning about those chemicals that are unintentionally released, that may travel great distances through the air, and that end up at high concentrations at the top of food chains. Given their tremendous habitat requirements and that of their prey (salmon), Northeastern Pacific killer whales are serving as sentinels of global pollution, and a reminder that we indeed inhabit a “global village.” ■

ESSAY 3.2

Infectious Disease and the Conservation of Biodiversity

Andy Dobson, Princeton University

■ Dissect any vertebrate, invertebrate, plant, or fungus and you will find a whole community of organisms living within their tissues; the richness of this community of parasites will increase as you examine the host's tissues at finer scales of resolution. Unfortunately, ecologists and conservation biologists often overlook the huge variety of biodiversity that lives in, upon, and often at the expense of free-living species. Parasites and microorganisms are a major component of biodiversity, perhaps making up as much as 50% of all living species (Price 1980; Toft 1991). Ironically, whereas few people worry about their long-term conservation (Sprenst 1992), it is important not to ignore parasites and pathogens, as many have profound effects that fundamentally influence the evolution of populations and the functioning of ecosystems.

The Zen of Parasitism

Parasites become problems when natural systems are perturbed, or when species escape regulation by their parasites; an important illustration of this occurs when invasive species escape from their natural pathogens. Green crabs (*Carcinus maenas*) host a significant diversity of parasites in their natural range along the Atlantic coast of Europe (Torchin et al. 2002). This parasite diversity is considerably reduced in the many areas of the world where green crabs have been accidentally introduced and have established as invading species. This absence of pathogens may make a significant contribution to the crab's ability to invade, as it considerably reduces the energy each crab puts into resisting the invasion of its body by a diversity of parasitic species. Indeed, in areas where crabs have successfully invaded they may grow to five times the size of the largest crabs found in their native range.

This effect appears to be an important general result; in detailed comparative studies of the most successful invasive animal species from a variety of taxa, Torchin et al. (2003) showed that parasite diversity is considerably reduced in areas where the species has invaded. Similar results were found in the fungal and viral pathogens of

plants that have invaded the United States (Mitchell and Power 2003). All of this suggests that the parasitic, under-observed half of biodiversity plays a major role in regulating the abundance of the more familiar free-living species.

Parasites can have dramatic effects at ecosystem levels. Rinderpest virus (RPV), a morbillivirus that causes widespread mortality in ungulates, was first introduced into East Africa at the end of last century with cattle (Plowright 1982). RPV spread throughout sub-Saharan Africa, producing mortality as high as 90% in some species. Travelers through the region report that in some places the ground was littered with carcasses and the vultures were so satiated they could not take off (Simon 1962). Even today, the observed geographic ranges of some species are thought to reflect the impact of the great rinderpest pandemic. Vaccination of cattle produced a remarkable and unforeseen effect; the incidence of RPV in wildebeest and buffalo declined rapidly and calf survival in these and other wild ungulates increased significantly (Talbot and Talbot 1963; Plowright 1982). This led to a rapid increase in the density of these species; in the Serengeti, wildebeest numbers increased from 250,000 to over a million between 1962 and 1976, and buffalo numbers nearly doubled over the same period and expanded their range. This increase in herbivore density produced a significant increase in some carnivore species, particularly lions and hyenas.

A significant threat to endangered species may be pathogens acquired from species with large populations that sustain continued infections. In this case, the pathogen is present in one host species and invades another, and two things can happen: The combined population densities of the potential host species may be insufficient to sustain the pathogen and it dies out, or the parasite sustains itself in the new community of hosts.

Pathogens with Multiple Hosts

When pathogens infect multiple host species it is likely that some hosts are more resistant to the pathogen than others; West Nile virus provides an impor-

tant example. Crow species are highly susceptible to the disease and die within a week of infection; in contrast, House Sparrows (*Passer domesticus*) seem more able to withstand infection (interestingly, House Sparrows are an invading species in the U.S.; their native range overlaps that of West Nile virus, suggesting the ghost of past natural selection for resistance [Campbell et al. 2002]).

At a further extreme, Nipah and Hendra virus have caused deadly outbreaks of disease in humans and domestic livestock in Australia, Malaysia, and Bangladesh. The main hosts of these viruses are fruit bats (*Pteropus hypomelanus*, *P. vampyrus*, and several other species), where the high levels of prevalence imply that they exist as a relatively benign pathogen. In undisturbed habitats, there is little contact between humans, their livestock, and bats. However, massive habitat conversion in Australia and Malaysia has compressed the range of fruit bats so that the only trees left for them to roost in are those associated with intensive agricultural areas. This increases rates of contact between bats and livestock or humans. Pathogen transmission usually occurs when fruits that the bats have been feeding on drop from trees and are consumed by pigs or horses. These partially infected fruits can trigger the first case of a disease outbreak, which spreads through the livestock into the agricultural workers and on to their families and friends. When this occurred in Malaysia, several million pigs had to be culled, and over a hundred humans were infected, more than 65% of whom died.

Pathogens that use multiple hosts create a double-edged problem for ecologists and conservation biologists. Pathogens like Nipah virus represent one extreme, where habitat conversion increases human exposure to novel pathogens. There is essentially no way of predicting when similar novel pathogens will emerge; all we can say is that the frequency of these events will increase as humans increase their rates of contact with novel environments and their potential hosts.

At the other extreme are multi-host pathogens that are vector transmitted and use mosquitoes, ticks, and fleas for

transmission between wildlife reservoirs and humans and their domestic livestock. The specificity of these pathogens is determined by the feeding choice of their vectors. In some cases this choice will be very specific and the pathogen will only occasionally spread from the reservoir into a novel host. This seems to be the case for West Nile virus, which is less of a problem in Europe, where it is transmitted predominantly by mosquitoes that specialize in birds. In the U.S., West Nile virus is transmitted by a hybrid mosquito that feeds on both birds and mammals. However, when vectors have a choice of hosts, the diversity of species present in a habitat will have a major buffering impact on the scale of an epidemic outbreak. Ostfeld and colleagues have shown that this is the case for Lyme disease in the U.S., where the diversity of hosts available for ticks leads to a significant reduction in the rate of attack on hosts that are susceptible to the disease (Ostfeld and Keesing 2000; LoGuidice et al. 2003). This buffering effect is even stronger for pathogens where the abundance of the vectors is independent of that of the hosts (Dobson 2004); this will be the case for mosquito-transmitted diseases such as malaria, Dengue fever, and West Nile virus. This creates an important incentive to conserve biodiversity, particularly in the event of future climate warming that will allow the classic tropical pathogens to spread to the temperate zone.

Most discussion of the response of vectored pathogens to climate change has focused on examining how increased temperature allow pathogens and mosquitoes to successfully complete their life cycle development in the temperate zone. Once the pathogen can develop in a shorter time period than the mosquitoes' life expectancy, the pathogen can establish. However, vectored pathogens will also be moving down a biodiversity gradient as they spread from the tropics to the temperate zone. There will be less choice for the mosquitoes, so they can focus their infective bites on the most common species; in many places this

will be *Homo sapiens* and their commensal domestic species.

Role of Predators in Buffering Outbreaks and Keeping Herds Healthy

Predators and scavengers may provide an unsuspected ecosystem service by preventing infectious disease outbreaks. Work by Packer et al. (2003) suggests that when predators selectively remove infected individuals from populations of prey species they will significantly reduce the burden of disease within the prey population; this may even lead to increases in the abundance of prey in the presence of predators! Evidence in support of this is provided in populations of game species where culling of predators has led to increases in infectious diseases and parasites as the host becomes more abundant. In studies of game birds in northern Britain the abundance of parasitic worms varies inversely with gamekeeper abundance (Hudson et al. 1992; Dobson and Hudson 1994). One of the gamekeeper's traditional jobs is to remove foxes and birds of prey; however these predators differentially remove heavily parasitized birds from the bird populations. Removing the foxes leads to a general increase in parasitic worm burdens that have a major impact on bird numbers.

In a similar fashion, the control of scavengers such as wolves, coyotes, and vultures may have permitted the emergence of prion diseases such as scrapie and chronic wasting disease in Europe and the U.S. (Prusiner 1994; Westaway et al. 1995). The natural foci of prion diseases seem to be areas characterized by very poor soils such as chalk grasslands. Ungulates that graze in these habitats are extremely nutrient stressed; they are particularly deficient in phosphorus and this leads them to chew on the carcasses of individuals who have failed to survive harsh winters. When scavenging canids are removed there are considerably more carcasses to chew on, and prion diseases that are present at very low levels in the population can slowly become

endemic at higher prevalences. Once they get into domestic livestock, they can produce devastating economic impacts (Anderson et al. 1996). They provide an important example of how previously obscure and little-known pathogens can quickly become quite significant when we perturb natural ecosystems.

To summarize, parasites and pathogens remain an important consideration in the management of captive and free-living populations of threatened and endangered species. Epidemiological theory suggests that pathogens shared among several species present a larger threat to the viability of endangered species than do specific pathogens. However, there is a way parasites and pathogens may be used to conservation advantage: Pathogens could be effectively employed as biological control agents to reduce the densities of introduced rats, cats, and goats that are a major threat to many endangered island species. Obviously, caution has to be exercised when considering introduction of any pathogen into the wild, so this method of pest control should be restricted to isolated oceanic islands (Dobson 1988). However, the majority of extinctions recorded to date in wild populations have occurred on oceanic islands (Diamond 1989).

Clearly, parasites and diseases are emerging as important considerations in conservation biology. The enormous expansion of our ecological understanding of parasites and their hosts in the last fifteen years means that ecologists now see a predictable structure in conditions that foster disease outbreaks. Epidemics can no longer be considered purely stochastic events that occur as random catastrophes. We now have a significant mathematical framework that delineates the general conditions under which a disease outbreak will occur (Anderson and May 1986, 1991; Grenfell and Dobson 1995). A major challenge for conservation biologists is to apply and extend this framework so it can minimize the disease risk to endangered species of plants and animals. ■

bined with nest predation by introduced cats, dogs, pigs, and rats. Of great concern is the likelihood that some threats may be **synergistic**, whereby the total impact of two or more threats is greater than what you would expect from their independent impacts (Myers 1987). Corals often are stressed physiologically by increases in

temperature, but may also be more susceptible to fungal pathogens when stressed (Harvell et al. 1999). This synergism suggests that the combined effects of global warming and increasing transport of disease organisms among coral reefs could precipitate catastrophic declines. At times, synergisms develop through the inter-

action of a threat and population density. In an experimental study, Linke-Gamenick and her colleagues (1999) showed that a toxic chemical reduced survivorship of a capitellid polychaete worm, but at high concentrations its impacts grew more severe with increasing density.

Further, many threats can intensify as they progress, a process known as “snowballing.” Invasion of plant communities in western Australia by the alien root pathogen *Phytophthora* causes death of woody species and an increase in herbaceous cover, which can suppress germination and early growth of woody seedlings (Richardson et al. 1996; Figure 3.3). The changes in the plant community in turn decrease the suitability of the community for many animal species, which may further reduce the capacity of the animal community to foster the development of woody cover. Thus, the initial inva-

sion pushes the entire system into a new balance that makes recovery of the original system difficult.

Finally, many species are threatened by interactions between large impacts, such as direct mortality from harvest, and more subtle impacts on their biology and population dynamics. For example, a variety of changes in the genetic structure of populations can enhance their risk of extinction. Species may lose functional genetic diversity due to prolonged isolation in small populations, or the loss of entire populations, which may leave them less able to cope with stresses of habitat degradation or climate change. These genetic threats, as well as many genetic tools for conservation are discussed in Chapter 11. Intrinsic demographic factors, such as rarity, low reproductive rates, or low dispersal rates can further predispose a population or species to extinction, as discussed later in this

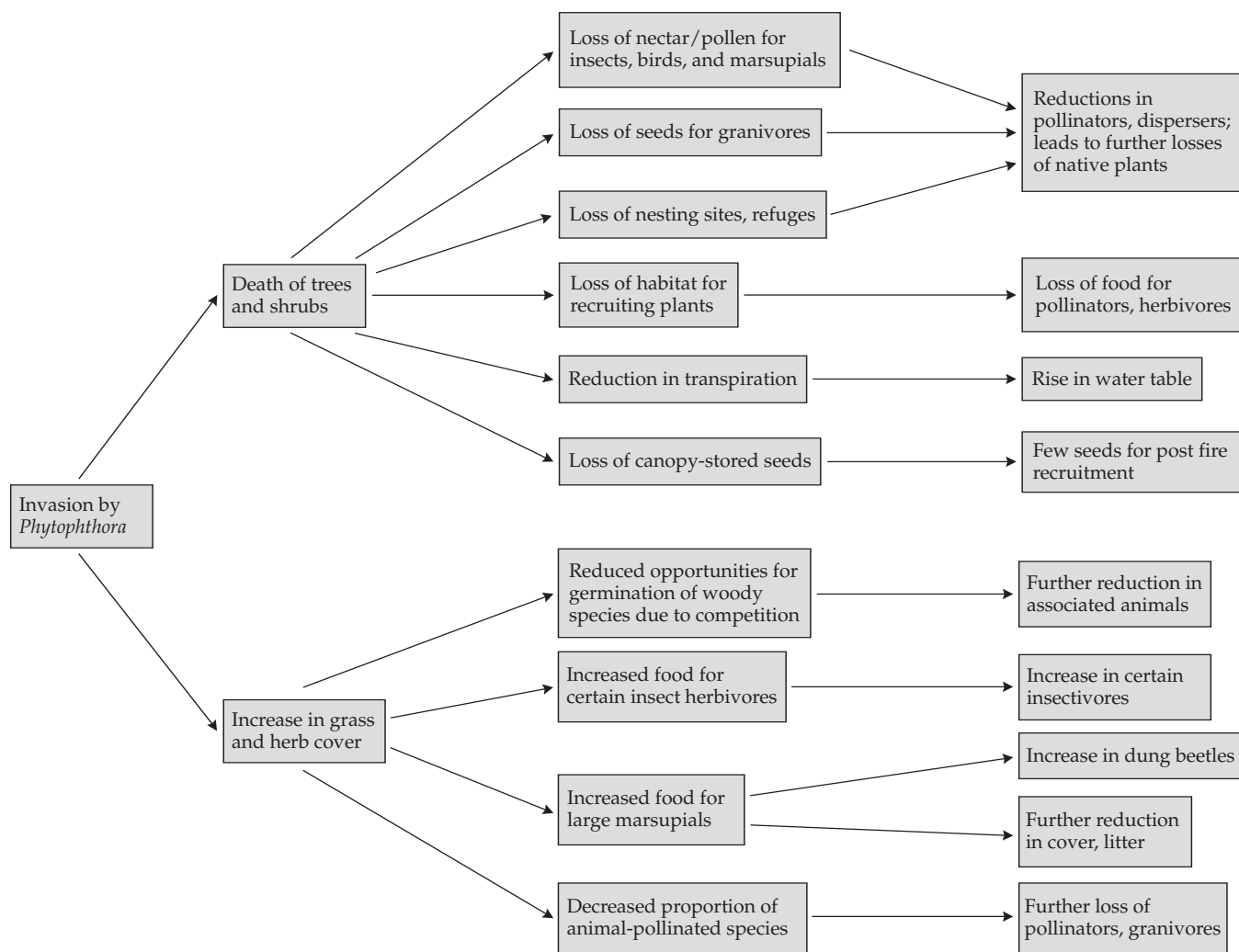


Figure 3.3 “Snowballing” effect of invasion of the alien root pathogen *Phytophthora cin-namomi* into shrublands and woodlands of western Australia. (Modified from Richardson et al. 1996.)

chapter and in Chapter 12. Importantly, species may vary in their responses to different threats based on their biology (Owens and Bennett 2000; Isaac and Cowlishaw 2004). Such demographic predispositions to risk can be exaggerated via reduced reproduction or increased mortality due to anthropogenic factors. Typically, both genetic and demographic threats interact with habitat and climate change, overexploitation, or species invasion to cause species loss, and ultimately changes in community and ecosystem function. Thus, although rarely the primary cause of extinction, genetic and demographic factors are important contributors to endangerment that must be considered in most conservation situations.

Anthropogenic Extinctions and Their Community and Ecosystem Impacts

The most obvious and extreme unwanted effects of human development are the extinction of species and populations, and transformation of natural ecosystems into degraded or even uninhabitable places. We can consider these the ultimate consequences of the expansion of human populations and consumption levels. Here, we will discuss patterns of extinction in some depth, and treat habitat transformation in detail in Chapter 6.

Extinction can be either global or local. **Global extinction** refers to the loss of a species from all of Earth, whereas a **local extinction** refers to the loss of a species in only one site or region. In addition, **ecological extinction** can occur when a population is reduced to such a low density that although it is present, it no longer interacts with other species in the community to any significant extent (Redford 1992; Redford and Feinsinger 2000). All these forms of extinction can affect remaining species, perhaps causing shifts in community composition, or ecosystem structure and function. Global extinction is the most tragic loss resulting from human activities, because once a species is lost entirely, it cannot be recreated.

Anthropogenic extinctions are caused directly through overexploitation, and also indirectly via habitat transformations that restrict the population size and growth of some species, or the introduction of species into new areas that over-consume or outcompete native species. Earliest human-caused extinctions were probably due to overexploitation, but increasingly habitat modification and introductions of invasive species to islands became primary causes. Only recently have other factors such as disease, pollution, and anthropogenic global climate change begun to play major roles as well. As we look to the future, synergisms among these factors and climate change are likely to accelerate extinction rates in the coming century (Myers 1987; Myers and Knoll 2001).

Because of the inherent spottiness of the fossil record, it is difficult to discern extinction events prior to record-

ed history, or to document the nature of changes to ecological communities. Our knowledge of prehistoric effects of humans on biodiversity is thus limited to a few cases where the fossil record can provide a clear trail, and to fairly gross-scale changes in ecosystems. Similarly, our incomplete knowledge of living taxa also makes this task difficult even after ecological records were kept in detail. Yet, some patterns are traceable.

Most notably, the Pleistocene extinction of megafauna (mammals, birds, and reptiles over 44 kg in body size) and other vertebrates speaks of widespread impacts of humans that have forever changed ecological communities. The demise of between 72% and 88% of the genera of large mammals in Australia, North America, Mesoamerica, and South America coincided with the arrival of humans in each continental region (44,000–72,000 years ago in Australia and 10,000–15,000 years ago in North and South America; Figure 3.4). Certainly the coincidence of pulses of human colonization or population growth and the loss of taxa is suggestive of a strong role of “Earth’s most ingenious predator” in the loss of these creatures (Steadman and Martin 2003). However, rapid climate change and concomitant vegetation change also took place in most cases (Diamond 1989; Guthrie 2003; Barnosky et al. 2004), and loss of many taxa in Alaska or Northern Asia where human populations were never large suggests that climate played a major, or in a few cases the only role in megafaunal extinctions (Barnosky et al. 2004).

Careful consideration of the evidence suggests that the loss of the megafauna may have resulted from a combination of range contraction due to climate change and decreases in population sizes due to hunting and habitat alteration by humans (see Figure 3.4). For example, mammoths often survived longest in areas without human populations. Although glaciations eventually caused extinctions of all mammoths, fragmentation of mammoth ranges among larger groups of Pleistocene human hunters may have tipped the balance for some populations (Barnosky et al. 2004). Both hunting and habitat change (e.g., burning of savannahs to improve game and forage conditions) seem the largest drivers of the demise of many large mammals in the conterminous United States (Martin 2001; Miller et al. 1999), resulting in more pronounced extinction events among these taxa than could be accounted for by climate change alone. Finally, humans were likely contributors to animal extinctions in Africa, although because human presence in Africa is so ancient, it is much more difficult to establish a causal link.

Dramatic extinction events occurred among birds as Polynesians colonized Pacific Islands 1000–3000 years ago. Over 2000 species (particularly flightless rails), and over 8000 populations were driven extinct by overexploitation, habitat alteration, and the introduction of rats, pigs, and other commensal mammals carried by the

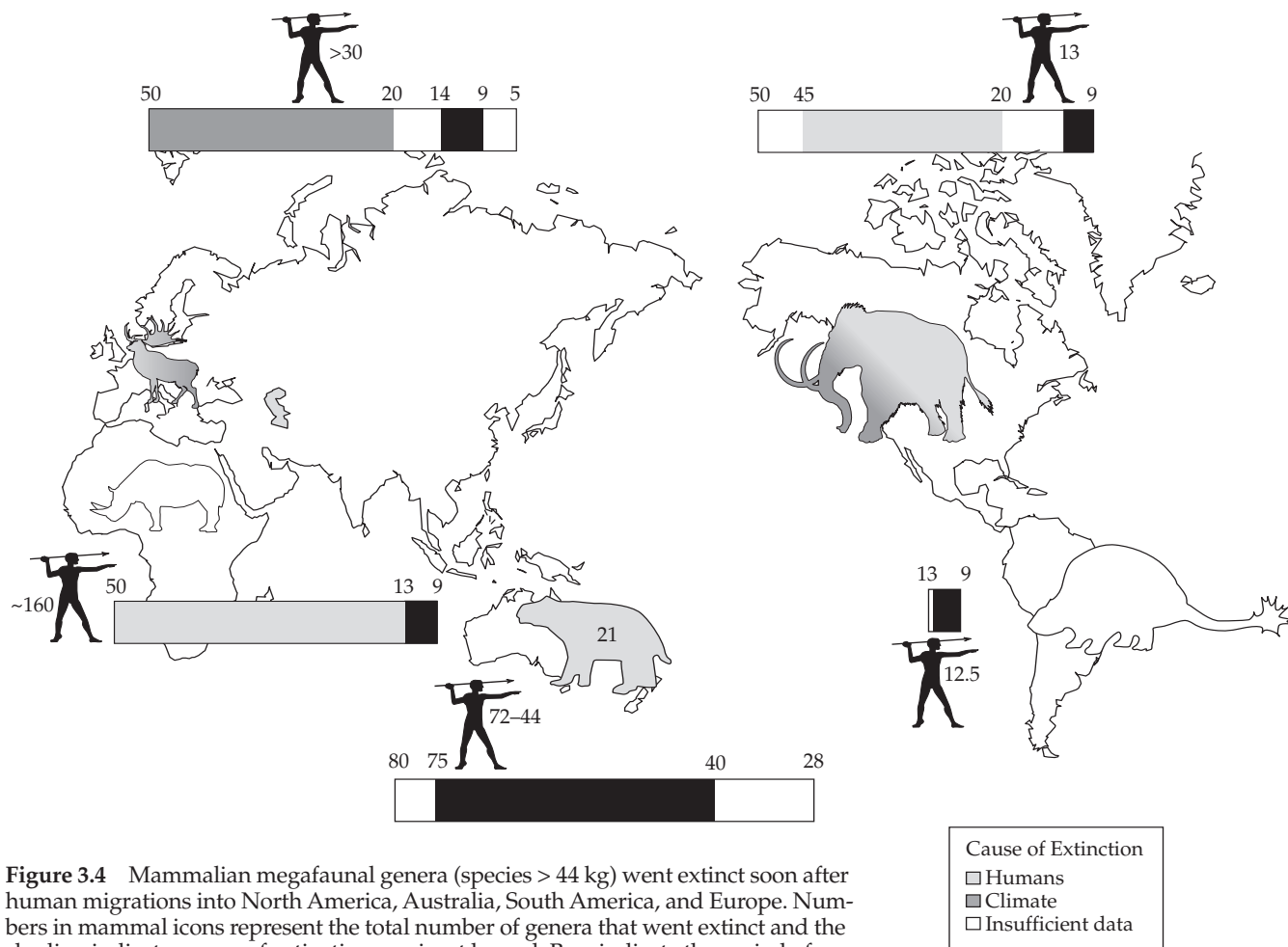


Figure 3.4 Mammalian megafaunal genera (species > 44 kg) went extinct soon after human migrations into North America, Australia, South America, and Europe. Numbers in mammal icons represent the total number of genera that went extinct and the shading indicates cause of extinction; see inset legend. Bars indicate the period of extinction (in kya), and shading indicates the magnitude of extinctions during that time; Black = many, dark gray = some, light gray = few, white = one or none. Numbers next to human icons indicate when humans arrived to the continent. Rapid climate warming (occurring from 14–10 kya) contributed to extinction in many cases, particularly in Eurasia and South America. In South America climate change and the arrival of humans entirely coincided with an extinction spasm of 50 genera. (Modified from Barnosky et al. 2004.)

Polynesians (Steadman 1995). In some cases, extinction occurred within the first 100 years after an island was colonized (Steadman 1995), while in others, species may have persisted for a thousand years, or to the present day (Steadman and Martin 2003).

A useful lesson emerges from study of the patterns of extinction among birds in the Pacific islands. Certain factors are correlated with rapid extinction of taxa, and others with their persistence or at least delayed extinction (Table 3.1). Most importantly, where humans introduced many species of predators (particularly rats), consumers, and certain weeds, and began cultivation, extinction was the predominant outcome among certain avian groups (Steadman and Martin 2003). In other words, where invasive species and habitat degradation were combined, extinctions were most common. Other abiotic and biotic

factors, such as the size and shape of islands and their species richness, were also predictors of extinction risk.

Somewhat surprisingly, patterns of extinction in more recent times are often obscure because despite the existence of historical records, few species were studied well enough for the causes of extinction to be understood. Further, many species particularly sensitive to human activities undoubtedly were lost before they were recorded, particularly across Europe, parts of China, and Africa or other locations with a long history of human occupation (Balmford 1996). Often the cases that are well understood are examples of rapid overexploitation, such as the extinction of Stellar's sea cow (*Hydrodamalis gigas*) and the Great Auk (*Pinguinus impennis*).

Birds are the only taxa for which causes of extinction can be ascribed in the majority of cases. Since 1500, we

TABLE 3.1 *Factors Influencing Vertebrate Extinction Following Human Colonization of Oceanic Islands*

	Promotes Extinction	Delays Extinction
Abiotic factors		
Island size	Small	Large
Topography	Flat, low	Steep, rugged
Bedrock	Sandy, noncalcareous, sedimentary	Limestone, steep, volcanics
Soils	Nutrient rich	Nutrient poor
Isolation	No near islands	Many near islands
Climate	Seasonally dry	Reliably wet
Biotic factors		
Plant diversity	Depauperate	Specie-rich
Animal diversity	Depauperate	Species-rich
Marine diversity	Depauperate	Species-rich
Terrestrial mammals	Absent	Present
Species-specific traits	Ground-dwelling, flightless, large, tame, palatable, colorful feathers, long and straight bones for tools	Canopy-dwelling, volant, small, wary, bad-tasting, drab feathers, short and curved bones
Cultural factors		
Occupation	Permanent	Temporary
Settlement pattern	Island-wide	Restricted (coastal)
Population growth and density	Rapid; high	Slow; low
Subsistence	Includes agriculture	Only hunting, fishing, gathering (especially in marine zone)
Introduced plants	Many species, invasive	Few species, noninvasive
Introduced animals	Many species, feral populations	Few or no species, no feral populations

Source: Modified from Steadman and Martin 2003.

know that at least 129 species went extinct (IUCN 2004). Habitat loss and degradation was a factor in most cases, particularly for species with narrow ranges. The introduction of alien invasive species, such as the black rat, was especially influential in the extinction of island endemics. Finally, overexploitation for food, feathers, or the pet trade, contributed to the demise of many species, including spectacular examples such as the massive overharvest of the Passenger Pigeon (*Ectopistes migratorius*) and Carolina Parakeet (*Conuropsis carolinensis*), both of which once had populations in the millions. As discussed above, extinction often was caused by a combination of two or more factors.

Indirect impacts of extinctions on animal and plant communities

As dramatic as these prior human-mediated extinction events have been, an equally dramatic adjustment of our concepts of “undisturbed” or “pristine” communities or ecosystems is now necessary. The extinction of large-bodied

species, as well as untold numbers of more poorly fossilized species, is likely to have caused significant changes in the composition, character, and extent of ecological communities. Further, ongoing extinctions of species or populations, and even the reduction of some species to low population sizes, are changing present-day ecosystems.

Where species depend on their interactions with other species, extinction can have ripple effects as these interactions are disrupted. Thus, the loss of key species can spark a suite of indirect effects—a **cascade effect** of subsequent, or **secondary extinctions**, and substantive changes to biological communities. Secondary extinctions, those caused indirectly by an earlier extinction, are most likely to occur when species rely on a single or a few species as prey or as critical mutualists. For example, a plant that relies on a single bat species for pollination will not be able to reproduce should that bat go extinct. Similarly, a carnivore specializing on two species of insects may be unable to maintain itself if one of its prey species went extinct.

BOX 3.1 Cascade Effects Resulting from Loss of a Critical Species or Taxon, or from Species Introductions

A wide variety of studies have shown that losses of a single or group of critical species can have a cascade effect on biological communities, with implications for the functioning of ecosystems. The loss of top predators is most commonly cited as causing cascade effects. Reduction of top predators typically results in increases in prey, and thus enhanced populations of medium-sized predators (mesopredators), which in turn leads to strong declines of their prey species (especially birds and mammals) (e.g., Palomares et al. 1995, Crooks and Soulé 1999, and Terborgh et al. 1999, 2001). Herbivore release from the loss of top predators can reduce plant populations and plant community diversity, which in turn reduces diversity of other herbivores (e.g., Estes et al. 1989, Leigh et al. 1993, and Ostfeld et al. 1996). Cascade effects can lead to the scavenger community as well (Berger 1999; Terborgh et al. 1999). Similar cascade effects have also been seen in food webs with insect top predators (Rosenheim et al. 1993; Letourneau et al. 2004), although these are much less studied, so little is known about the commonness of these effects.

Studies of lake ecosystems has repeatedly shown that loss of piscivo-

rous fishes release fish that graze on zooplankton, leading to a reduction in zooplankton, increases in phytoplankton, and broad rearrangements in community composition (e.g., Carpenter et al. 1985, Vanni et al. 1990, Carpenter et al. 2001, and Lazzaro et al. 2003). Effects can include changes in water clarity and large scale shifts in macroinvertebrate abundance and diversity (Nicholls 1999). Importantly, cascades do not always occur when piscivorous fish are removed, but only under specific conditions (Benndorf et al. 2002). Both ecosystem and community level effects can result from the loss of anadromous fishes. In the northwest of North America reduction in, or loss of, salmon populations can cause decreases in the input of nutrients to inland streams (Schindler et al. 2003), and loss of food for grizzly bears, bald eagles, killer whales, and predaceous fishes (e.g., Francis 1997 and Willson et al. 1998).

The loss of large-bodied species can often cause ripple effects through a community. Many studies in tropical forest have documented that the loss of many large-bodied species preferred by hunters leads to release of their prey, and loss of any services to other community members (Dirzo and

Miranda 1991; Redford 1992; Redford and Feinsinger 2001). Reduction of plant diversity can result through enhanced granivory and herbivory (Terborgh and Wright 1994; Ganzhorn et al. 1999), or through loss of seed dispersal, and sometimes pollination, services (e.g., Chapman and Onderdonk 1998, Andersen 1999, Hamann and Curio 1999, and Wright et al. 2000).

Many cascade effects can be caused by changes in the abundance of ecosystem engineers. Loss of ecosystem engineers results in large structural changes in ecosystem, such as loss of pools created by beavers (Naiman et al. 1988), or shifts in plant diversity with loss of grazing by bison (Knapp et al. 1999). Loss of detritivores in streams can also cause large-scale changes (Flecker 1996).

Finally, cascade effects can result from species introductions. Introduction of species to marine estuaries or to lake systems has been shown to result in massive reduction in native algae, loss of native crayfish, molluscs, and other invertebrates, and even in a reduction in waterfowl, fishes, and amphibians (e.g., Olsen et al. 1991, Hill and Lodge 1999, and Nyström et al. 2001).

Cascade effects are probable in any community where strong interactions among species occur, be they predator-prey, mutualistic, or competitive in character, and thus are likely to have occurred prior to recorded history as well as in the few recorded cases from recent times (Box 3.1). One of the best-known examples of a cascade effect occurred when local extinction of sea otters (*Enhydra lutris*), which were aggressively hunted for their pelts, led to a transformation of marine kelp forest communities off the Pacific coast of North America (Estes et al. 1989). Sea otters are heavy consumers of sea urchins, and their absence led to an urchin population explosion, which in turn leads to overgrazing of kelp and other algae by the urchins, creating "urchin barrens" (Estes et al. 1989). Thus, because kelp forests are a haven for a broad variety of fishes and other species (Dayton et al. 1998), the local extinction of sea otters leads to the local extinction of many other species, and a radical change in the nature of the structure and composition of the community.

Cascade effects are difficult to demonstrate in the hyper-diverse tropics, but are likely to occur there. Tropical forests in which species have been driven locally extinct ("empty forests," Redford 1992) or depleted ("half-empty forests," Redford and Feinsinger 2001) now may lack effective populations of key interactors. The loss of critical seed dispersers could eventually result in the extinction of disperser-dependent tree species (Janzen 1986; see Essay 12.3). Depletion of top predators may cause the **ecological release** of prey species that may in turn drive down populations of their prey, as occurred with sea otters (Terborgh et al. 1999; see Case Study 7.3). Thus, many tropical communities may appear healthy on the surface, but are in fact destined to decline in diversity due to disruption of critical interactions through local extinction of pollinators, seed dispersers, and top predators.

Overexploitation of great whales from 1700 to the mid-1900s had enormous impacts on marine ecosystems

(Roberts 2003). The removal of such large consumers released their prey, causing changes throughout the food chain. Industrial-scale fishing of large-bodied fish species that occupy higher places on the food chain also has initiated dramatic cascading effects throughout marine ecosystems (Dayton et al. 1995; Parsons 1996). The net result may be marine communities that bear little resemblance to the structure and abundances that would have been typical before humans began whaling and fishing on extensive scales (Pauly et al. 1998). Presumably, the loss of megafauna in the Pleistocene had similar community-level impacts to those that we can describe from more contemporary events.

Although it would be helpful in conservation to know which species are most critical to communities, in practice it is not simple to identify which species have the largest impacts, or are involved in the greatest number of strong interactions (Berlow et al. 1999). **Dominant species** are those that are very common and that also have strong effects on other members of the community (Figure 3.5). Examples include reef-building corals, forest trees, and large herbivores, such as deer. **Ecosystem engineers**, those species such as beavers or elephants that strongly modify habitat, are also ones whose absence or presence will change communities (Naiman et al. 1986; see Case Study 9.1). Generally, both community dominants and ecosystem engineers are relatively easy to identify.

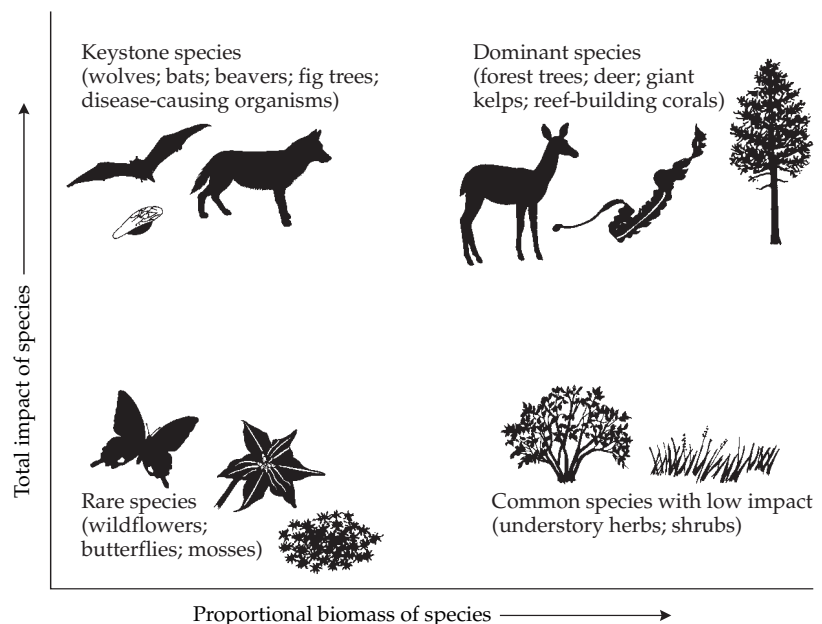
A **keystone species** is a species that has a greater impact on its community than would be expected by the contribution of its overall numbers or biomass (Paine 1969; Power et al. 1996; see Figure 3.5). If a bat species is necessary for pollinating many species, and no other

species can serve its role, then it would be considered a keystone species. Similarly, large carnivores frequently act as keystone species through their impacts on other predators, a wide variety of prey species, and the competitors of their prey (Crooks and Soulé 1999). Ecosystem engineers are usually also keystone species, as defined above. Unfortunately, unlike dominant species whose impacts are easily discernable, often a keystone species is not so easily recognized and is only discovered after its numbers have been reduced and the impacts become obvious.

Current Patterns of Global Endangerment

As we consider the present era, the challenges to biodiversity have intensified in many respects. Where prehistoric impacts were dominated by overexploitation, moderate habitat modification, and introduction of human commensals, in recorded history we add the problems of pollution and human infrastructure development, and ultimately human-mediated climate change. In our era, vastly larger human populations and greater consumptive habits ensure that each primary threat has increased in magnitude and extent. In Chapter 6 we will examine how these threats have resulted in habitat degradation across the globe, but here we will focus on effects on species. To help us direct our efforts, and to help motivate social and political will to act on this biodiversity crisis, it may help to review what is known about global patterns of species endangerment, as well as those of selected countries.

Figure 3.5 Keystone and dominant species can have large impacts on biological communities. Keystone species by definition make up only a small proportion of the biomass of a community, yet have a large impact, whereas dominant species have impacts that are more proportional to their biomass or abundance. Reductions in the biomass or extinction of keystone or dominant species can be expected to cause cascade effects in communities. Many rare and common species have low impacts, and changes in their abundance may not have noticeable effects on other species. (Modified from Power et al. 1996.)



Globally threatened species

The best data on global endangerment are collated in the IUCN Red List of Threatened Species (www.redlist.org). The Red List classifies all species reviewed into one of nine categories (Box 3.2), with three primary categories of endangerment, in order of the risk of extinction: Critically Endangered (CR), Endangered (EN), and Vulnerable (VU). Very specific rules have been adopted to standardize rankings of each species, and to allow use of the list to index changes in the status of biodiversity over time (see Box 3.1, Table A; IUCN 2001). Taxonomic experts, conservationists, and other biologists work together in teams to conduct the reviews, and thus assure that the best available information is used in each case, although large uncertainties due to incomplete knowledge often make judgments difficult. Thus, the Red List is seen as a work in progress, undergoing constant revision both to document true changes in status, and to reflect updates in our knowledge. Through these efforts, the IUCN Red List has become the most complete database on global status of species available.

Complete evaluations have been undertaken for bird and amphibian species, and are nearly complete for mammals, and gymnosperms (conifers, cycads, and ginkgos) among plants. However, only a small percentage of all other taxa have been reviewed (about 6% of reptiles and fishes; 0%–3% of invertebrates, and 1%–5% of other plant groups; Table 3.2). Overall only 2.5% of described species have been evaluated. Among those species that have been evaluated, many are so poorly known that they cannot be categorized, and are given a Data Deficient ranking (9.5%; see Box 3.1).

Of the 38,046 species evaluated as of November 2004, 41% are endangered (CR, EN, or VU), 10% are Near Threatened or Conservation Dependent (meaning they may become endangered in the coming decades), while 38% are designated as Least Concern (indicating a very low risk of extinction for the foreseeable future). The Red List also includes a conservative tally of extinction, recording a total of 784 extinctions, plus 60 extinctions in the wild (where the only living individuals are in captivity or cultivation) (Baillie et al. 2004). Globally, 317 ma-

TABLE 3.2 *Number of Globally Threatened Species by Taxon*

	Described species	Evaluated species	Threatened species	Percent of described species threatened	Percent of evaluated species threatened
Vertebrates					
Mammals	5416	4853	1101	20	23
Birds	9917	9917	1213	12	12
Reptiles	8163	499	304	4	61
Amphibians	5743	5743	1856	32	32
Fish	28,600	1721	800	3	46
Invertebrates					
Insects	950,000	771	559	0.1	73
Molluscs	70,000	2163	974	1	45
Crustaceans	40,000	498	429	1	86
Others	130,200	55	30	0.02	55
Plants					
Mosses	15,000	93	80	0.5	86
Ferns	13,025	210	140	1	67
Gymnosperms	980	907	305	31	34
Dicotyledons	199,350	9473	7025	4	74
Monocotyledons	59,300	1141	771	1	68
Lichens	10,000	2	2	0.02	100
Total	1,545,594	38,046	15,503	1	41

Note: A "threatened species" includes any species designated as CR, EN, or VU by the IUCN Red List.

Source: Modified from IUCN 2004.

BOX 3.2 The IUCN Red List System

The IUCN Red List System, a systematic listing of species in threat of extinction, was initiated in 1963 to be used in conservation planning efforts around the globe. Over time, hundreds of scientists have worked to create listing criteria that have been carefully defined to be maximally useful as a diagnostic tool to help establish extinction risk over all taxa. Species are assigned to one of nine categories, which indicate their threat status or their status in the review process (Figure A). These categories are defined as follows:

Extinct (EX)

A taxon is Extinct when there is no reasonable doubt that the last individual has died. A taxon is presumed extinct when exhaustive surveys in known and expected habitat, at appropriate times (diurnal, seasonal, annual) to the taxon's life cycle and life form, throughout its historic range have failed to record an individual.

Extinct in the Wild (EW)

A taxon is Extinct in the Wild when it is known only to survive in cultivation, in captivity, or as a naturalized population (or populations) well outside the past range, and there is no reasonable doubt that the last individual in the wild has died, as outlined under EX.

Critically Endangered (CR)

A taxon is Critically Endangered when the best available evidence indicates

that it meets any of the criteria A–E in Table A for Critically Endangered species, and is therefore facing an extremely high risk of extinction in the wild.

Endangered (EN)

A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A–E for Endangered (see Table A) and is therefore facing a very high risk of extinction in the wild.

Vulnerable (VU)

A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A–E for Vulnerable (see Table A) and is therefore facing a high risk of extinction in the wild.

Near Threatened (NT)

A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered, or Vulnerable now, but is close to qualifying for or is likely to qualify for a threatened category in the near future.

Least Concern (LC)

A taxon is deemed Least Concern when it has been evaluated against the criteria and it neither qualifies for the previously described designations (Critically Endangered, Endangered, Vulnerable, or Near Threatened), nor is it likely to qualify in the near future.

Widespread and abundant taxa are included in this category.

Data Deficient (DD)

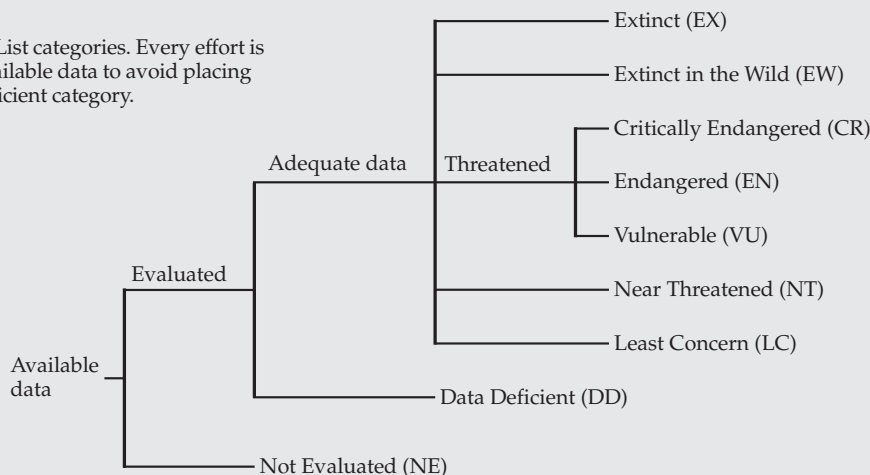
A taxon is Data Deficient when there is inadequate information to make a direct or indirect assessment of its risk of extinction based on its distribution, population status, or both. Every effort is made to use this category as a last resort, as this is not a category of threat, but only indicates more information is needed to make a status determination.

Not Evaluated (NE)

A taxon is Not Evaluated if it has not yet been evaluated against the criteria.

Assignment to one of the three threatened categories (CR, EN, or VU) is made on the basis of a suite of quantitative standards adopted in 1994 that relate abundance or geographic range indicators to extinction risk (see Table A). The different criteria and their quantitative values (A–E) were chosen through extensive scientific review, and are aimed at detecting risk factors across the broad diversity of species that must be considered (IUCN 2001). Qualification under any of the criteria A–E is sufficient for listing; however, evaluations are always made as completely as possible for use in evaluating changes in status over time, and for conservation planning purposes. Thus, the status of a taxon will be evaluated according to most of these criteria, as

Figure A IUCN Red List categories. Every effort is made to employ all available data to avoid placing species in the Data Deficient category.



far as is possible given current knowledge.

A major advance in risk evaluation, the Red List criteria require efforts to place quantitative bounds on our knowledge, and explicitly allow for uncertainty. The assignments to category are not assignments of priority,

but rather a reflection of our current best judgment of how great the risk of extinction is for this species, given the best available information at present. All species on the list must be reevaluated at least once every ten years.

In addition to quantifying risk of extinction, the Red List compiles data

on the nature of the threats to the species. These evaluations are useful for initial efforts to conserve the threatened species, and in aggregate can guide efforts to reduce threatening processes.

TABLE A Overview of Criteria (A–E) for Classifying Species as CR, EN, or VU in IUCN Red List

Criterion	Critically Endangered (CR)	Endangered (EN)	Vulnerable (VU)	Qualifiers
A.1 Reduction in population size	>90%	>70%	>50%	Over 10 years or 3 generations in the past where causes are reversible, understood, and have ceased
A.2–4 Reduction in population size	>80%	>50%	>30%	Over 10 years or 3 generations in the past, future, or combination, where causes are not reversible, not understood, or ongoing
B.1 Small range (extent of occurrence)	<100 km ²	<5000 km ²	<20,000 km ²	Plus two of (a) severe fragmentation or few occurrences (CR = 1, EN = 2–5, VU = 6–10), (b) continuing decline, (c) extreme fluctuation
B.2 Small range (area of occupancy)	<10 km ²	<500 km ²	<2000 km ²	
C Small and declining population	<250	<2500	<10,000	Mature individuals, plus continuing decline either over a specific rate in short time periods, or with specific population structure or extreme fluctuations
D.1 Very small population	<50	<250	<1000	Mature individuals
D.2 Very small range	—	—	<20 km ² or <5 locations	Capable of becoming CR or EX within a very short time
E Quantitative analysis	>10% in 100 years or 3 generations	>20% in 20 years or 5 generations	>50% in 100 years	Estimated extinction risk using quantitative models, e.g., population viability analyses

Source: IUCN 2001.

rine, 2981 freshwater, and 13,657 terrestrial species are considered endangered, and recorded extinctions are similarly apportioned.

For the most complete evaluated taxa, amphibians and gymnosperms stand out as particularly threatened (see Table 3.2). Cycads, an ancient group of gymnosperms, are especially vulnerable, with 52% endangered. The true level of threat is undoubtedly higher than these estimates due to the large number of Data Deficient rankings: 1290 amphibians (23%), 360 mammals, 78 birds and 77 gymnosperms all are too poorly known to be ranked, but certainly some of these are endangered.

Among mammals, ungulates, carnivores, and primates are particularly at risk mostly due to habitat degradation and overexploitation (Baillie et al. 2004). Albatrosses, cranes, parrots, pheasants, and pigeons are particularly threatened among the birds due to bycatch, habitat loss, the pet trade, and direct exploitation (Birdlife International 2004). Amphibians appear to be at greatest risk of extinction, with a high fraction of these species listed as critically endangered (21%; IUCN 2004). A wide variety of threats affect amphibian populations throughout the world, many of which exert synergistic effects on these sensitive animals; these threats

are described by Joe Pechmann and David Wake in Case Study 3.1.

While levels of endangerment among the remaining groups reflect a tendency for worrisome cases to be put forward for evaluation ahead of general analyses (for example, see crustaceans and mosses in Table 3.2), it seems likely that high levels of threat may occur in many other groups. Turtles and tortoises have been more completely assessed among the reptiles, and 42% are endangered (Baillie et al. 2004). Marine and freshwater fishes are placed on the list in increasing numbers, suggesting a serious level of threat, whatever the exact percentage. Two messages from these statistics are clear: First, a large fraction of vertebrate and gymnosperm diversity is in great danger of extinction over the next century, and second, we know very little about the status of most other taxa.

Globally threatened processes

Not only are species at risk of extinction, but some processes that undergird ecosystem functions, or that are glorious in and of themselves, are put at risk from human activities. Lincoln Brower discusses the concept of an “endangered biological phenomenon,” in which a species is likely to survive, but some spectacular aspect of its life history, such as the mass annual migration of monarch butterflies between Mexico and the United States, is in jeopardy of disappearing (Essay 3.3). The mass migrations of springbok in southern Africa have already been eliminated but the seasonal migrations of vast herds of wildebeest and zebra in the Serengeti still exist. Not only is this mass migration an amazing spectacle, but the Serengeti grasslands are adapted to the impacts of high densities of these grazers, as well as other ungulates. The loss of wildebeest migra-

tions would be tragic, even though wildebeest would survive in many places.

What factors are most threatening to biodiversity globally?

As species are evaluated, all threats faced at present or in the past that led to endangerment are coded into the Red List database. Our knowledge about the threats faced by species varies tremendously as certain types of threats are easier to document (e.g., forest conversion versus competition from invasive species), and for some species it is only possible to say that they are declining and endangered, but not to diagnose why. Most species face multiple threats. Finally, the red list is dominated by evaluations primarily for vertebrates and some vascular plants, and for areas where many biologists already work, perhaps reflecting biases in interest among biologists more than intrinsic levels of threat (Burgman 2002). Thus, we cannot be sure that the patterns that may hold for birds will serve for mollusks and other species groups (and indeed, we should expect that they will not in many cases). Nonetheless, to a limited degree, we can use these data to give us a sense of the pervasiveness of different types of threats.

Habitat loss and degradation is the most pervasive and serious threat to mammals, birds, amphibians, and gymnosperms (Figure 3.6). Overexploitation is the most pervasive threat to fishes, and a predominant one for mammals and birds as well, whereas invasive species pose particular risks for birds on islands (Baillie et al. 2004). Amphibians are more challenged than birds and mammals by pollution that directly kills individuals, and by changes in the abundance of native species, particularly diseases. Intrinsic factors, such as a limited reproductive capacity or limited

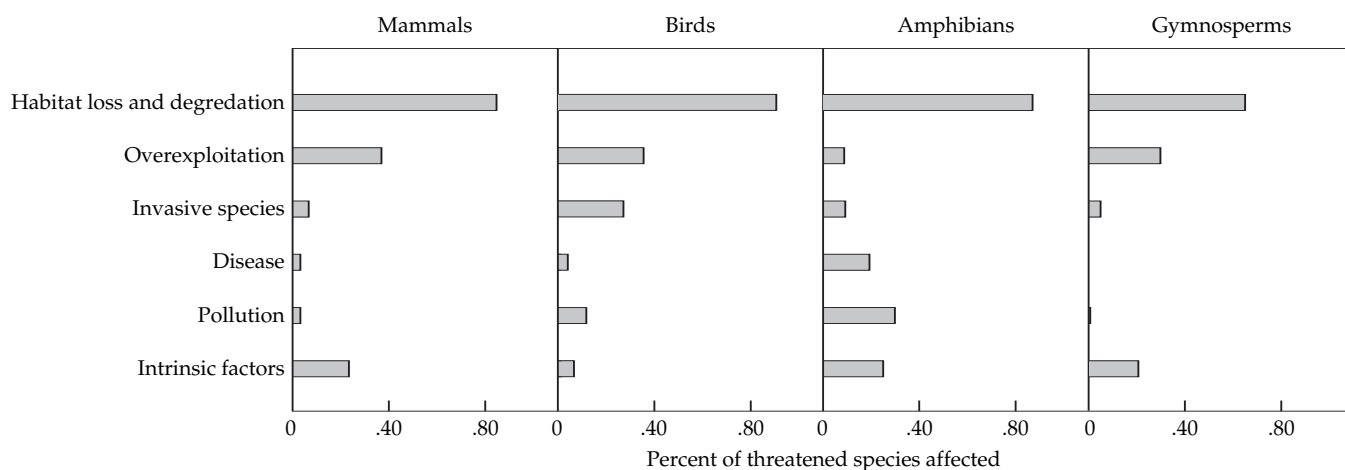


Figure 3.6 Habitat loss and degradation is the greatest threat to global biodiversity among mammals, birds, amphibians, and gymnosperms. Because not all threats are documented, this figure underestimates threat levels among Red Listed species. Overexploitation includes both direct mortality and by-catch. (Modified from IUCN 2004.)

ESSAY 3.3

An Endangered Biological Phenomenon

Lincoln P. Brower, *Sweet Briar College*

■ Much of conservation research focuses on describing diminishing species diversity and on understanding the processes that lead species to small populations, and thence to extinction. Here I discuss endangered biological phenomena, defined as a spectacular aspect of the life history of an animal or plant species, involving a large number of individuals, that is threatened with impoverishment or demise. The species per se need not be in peril; rather, the phenomenon it exhibits is at stake (Brower and Malcolm 1991).

Examples of endangered biological phenomena include the ecological diversity associated with naturally flooding rivers, the vast herds of bison of the North American prairie ecosystems, the synchronous flowering cycles of bamboo in India, the 17-year and 13-year cicada emergence events in eastern North America, and scores of current animal migrations. Instances of the latter include seasonal migrations of the African wildebeest and North American caribou, the wet and dry season movements of Costa Rican sphingid moths, the billion individuals of 120 songbird species that migrate from Canada to Neotropical overwintering areas, and the highly disrupted migrations of numerous whale species.

There are two principal reasons why animal migrations are endangered by human activities. First, migrant species move through a sequence of ecologically distinct areas, any one of which could become an Achilles' heel. Second, aggregation of the migrants can occur, making the animals especially vulnerable. The major impact on migratory species is due to accelerating habitat modification throughout the world. Even when problems are recognized, mitigation is difficult because of varying policies and enforcement abilities in the different countries the animals occupy during the different phases of their migration cycles. The extraordinary migration and overwintering behaviors of the monarch butterfly in North America well exemplify the concept of endangered phenomena.

The monarch butterfly (*Danaus plexippus*) is a member of the tropical subfamily Danainae, which contains 157 known species. It is alone in its subfam-

ily for having evolved extraordinary spring and fall migrations (Figure A) that allow it to exploit the abundant *Asclepias* (milkweed) food supply across the North American continent, becoming one of the most abundant butterflies in the world. Remarkably, and in contrast to vertebrate migrations, the monarch's orientation and navigation to its overwintering sites is carried out by descendants three or more generations removed from their migrant forebears. Its fall migration, therefore, is completely inherited, with no opportunity for learned behavior. This, together with the vastness of the migration and overwintering aggregations, constitutes a unique biological phenomenon.

Two migratory populations of the monarch occur in North America. The

larger one occurs east of the Rocky Mountains and undoubtedly represents the stock from which the smaller, western North American migration evolved. Both migrations are threatened because the aggregation behavior during winter concentrates the species into several tiny and vulnerable geographic areas.

By late summer, the monarch population in eastern North America builds to an estimated 0.5–3 billion individuals over an enormous area east of the Rocky Mountains. Beginning in late August, the adult butterflies migrate to central Mexico, where they overwinter for more than five months in high-elevation fir forests, about 90 km west of Mexico City (see Figure A). Here the butterflies coalesce by the hundreds of millions into dense and stunningly spectacular aggregations that festoon

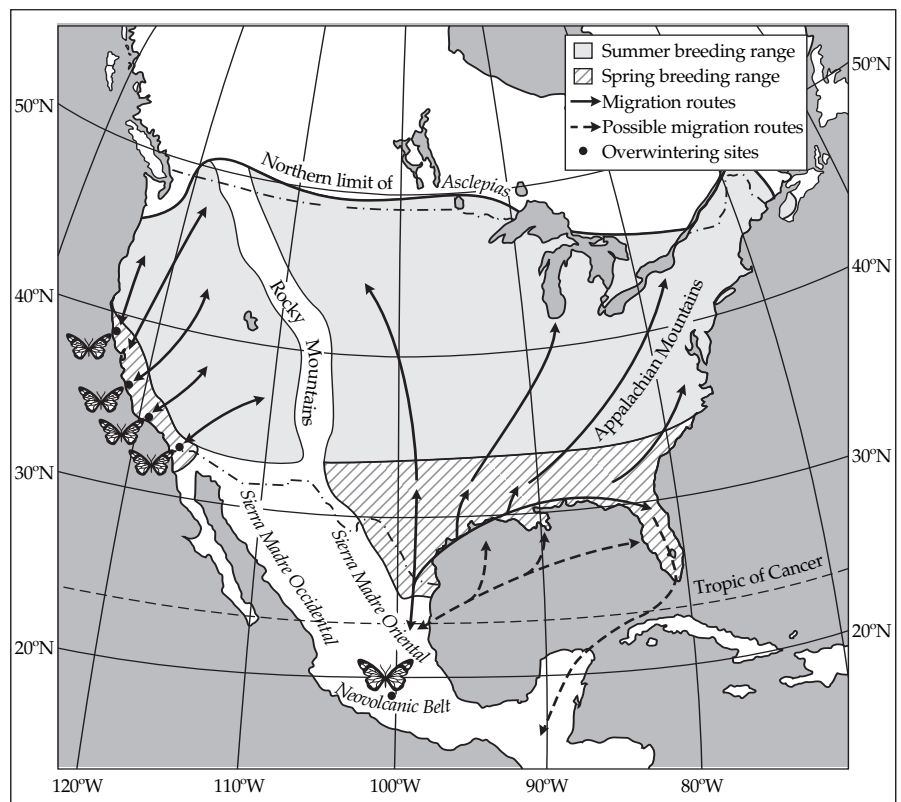


Figure A Fall and spring migrations of the eastern and western populations of the monarch butterfly in North America. (Modified from Brower 1995.)

0.1 to 5 hectares of forest. The butterflies, effectively in cold storage, remain sexually inactive until the approach of the vernal equinox.

Survivors from the Mexican overwintering colonies begin migrating northward in late March to lay their eggs on sprouting milkweed plants (*Asclepias* spp.) (see Figure A). These 8-month-old remigrants then die and their offspring, produced in late April and early May, continue the migration northward to Canada. Over the summer, two or three more generations are produced as each previous generation dies. Toward the end of August, butterflies of the last summer generation enter reproductive diapause and the cycle begins anew as these monarchs migrate instinctively southward to the

overwintering grounds in Mexico.

To date, about 30 overwintering areas have been discovered on 12 isolated mountain ranges in central Mexico at elevations ranging from 2900 to 3400 m. This elevational band coincides with a summer fog belt where boreal-like oryamel fir (*Abies religiosa*) forests occur that probably are a relict ecosystem from the Pleistocene. The five largest and least disturbed butterfly forests occur in an astoundingly small area of 800 km². By clustering on the trees in the cool and moist environment, individual monarchs are able to survive in a state of reproductive inactivity until the following spring.

Until recently, human impact on the high-elevation fir forests has been less than that on other forest ecosystems in

Mexico. However, negative developments began to occur in the 1970s.

Commercial harvest of trees, including thinning and clear-cutting has increased illegal removal of logs and firewood, and local charcoal manufacturing in pits dug within the fir forest. Villages have expanded, reaching locations up the mountainsides, and this expansion has led to an increased frequency of fires associated with forest clearing for planting corn and oats, and also with killing young trees for local home construction. Forest lepidopteran pests have invaded some areas of the fir ecosystem, probably due to stress caused by thinning and deforestation at lower elevations. As a result of increasing lepidopteran pests, spraying of the organic pesticide, *Bacillus thuringiensis*,

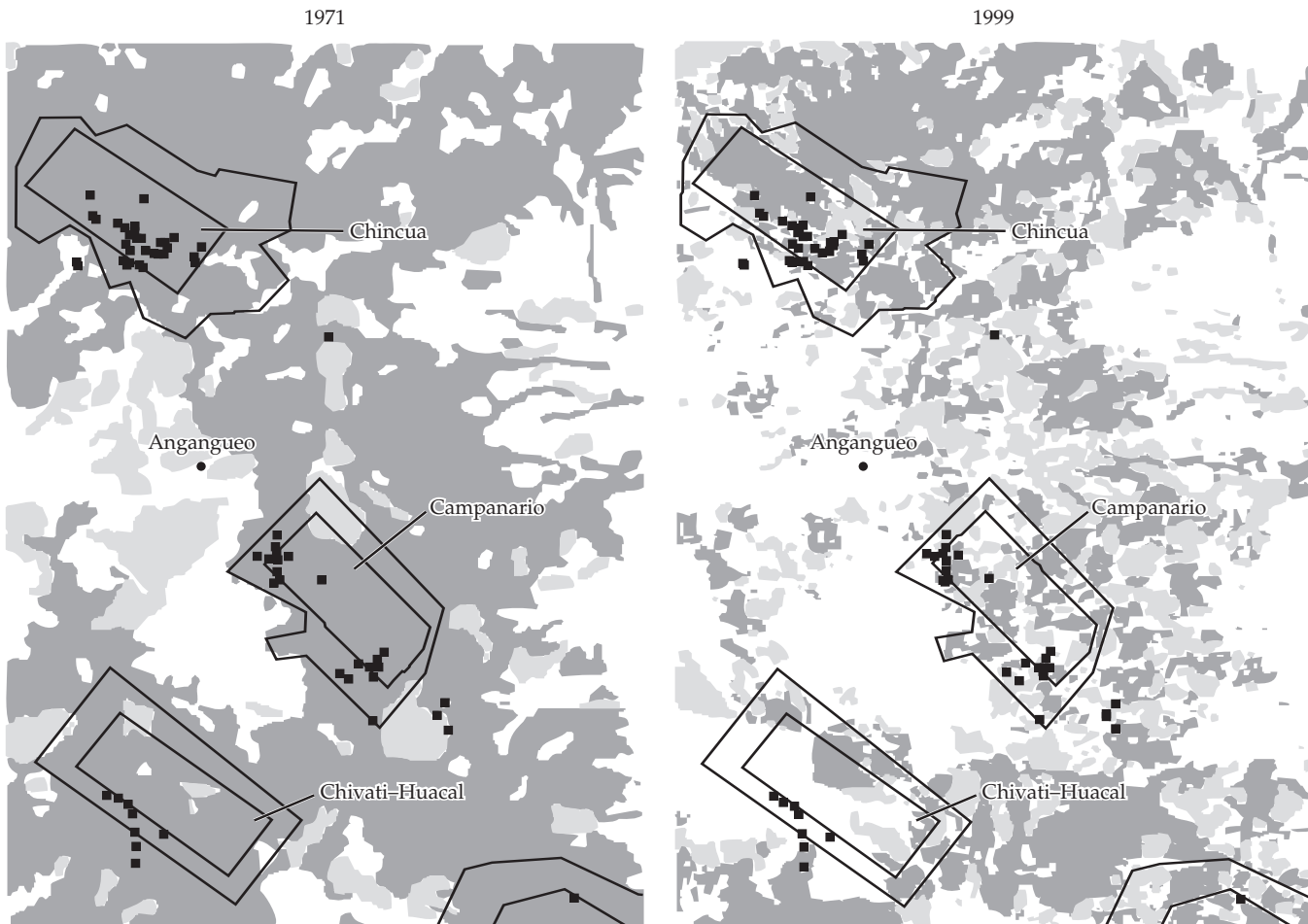


Figure B Forest cover has dropped dramatically within, and adjacent to, the three major monarch butterfly reserves from 1971 to 1999. Forest is shown in dark gray, forest habitat that is somewhat degraded is shown in light gray, and highly modified areas are in white. Squares denote any butterfly overwintering sites that have been recorded, but not all those shown persist today. For each reserve, the inner line denotes core areas and the outer line buffer zones. (Modified from Brower et al. 2002.)

was initiated and considered for widespread use without adequate knowledge of its effect on monarchs. Most recently, heavy ecotourism is trampling the infrastructure and generating severe dust precipitation on vegetation along paths through the colonies; because of the income generated, there is demand to open all colonies to tourists.

Encroachment on existing monarch overwintering sites, even those in reserved status, has been extensive in the past two decades. A comparison of photos from 1971 and 1999 show shocking reductions in forests both outside and inside some of the largest and most important reserves (Figure B; Brower et al. 2002). The remaining fragments of forests experience a disrupted microclimate that will not support the butter-

flies once fragments become too small or perforated via selective logging.

As a result of documenting these drastic habitat losses, in November 2000, then President Ernesto Zedillo accepted recommendations to revise and increase the area protected to a total of 56,259 ha and to redefine the area as the "Monarch Butterfly Biosphere Reserve" (Brower et al. 2002). Importantly, this new decree was associated with a trust fund to compensate local inhabitants for the profits they would have made through logging. Notwithstanding this new decree, illegal logging has accelerated and is severely degrading critical areas of the reserve (Galindo and Honey-Roses 2004). Conservation of this migratory phenomenon will not succeed without enforcement of logging bans together

with appropriate compensation to affected people. Public education about the values of protecting these forests and the remarkable spectacle of nature that the monarch butterfly migrations represent is desperately needed.

If we fail to conserve these overwintering sites, we will not lose the monarch butterfly as a species, because numerous nonmigratory populations will persist in its tropical range. However, the monarch's spectacular North American migrations will soon be destroyed if extensive overwintering habitat protection and management are not implemented on a grand scale. The impending fate of this remarkable insect is an omen, warning us that we must incorporate the concept of endangered biological phenomena into our plans for conserving biodiversity. ■

dispersal ability, are critical factors in endangerment for a large number of species as well (see Figure 3.6).

Where are species most at risk worldwide?

Some biomes contain greater fractions of threatened species, particularly biomes that are already species rich (Figure 3.7). Tropical and subtropical moist and dry forests, grasslands, savannas, shrublands, montane grasslands, and xeric biomes all have substantial numbers of threatened mammals, birds, and amphibians. As global climate change intensifies, many worry that montane habitats in particular will become unsuitable for many species, greatly increasing biodiversity losses.

Across the globe, there are particularly high numbers of threatened species in South America, Southeast Asia, sub-Saharan Africa, Oceania, and North America (IUCN 2004). To a large degree, this distribution reflects the vastly greater numbers of species in the tropics, as well as intensifying pressures, particularly in Southeast Asia and sub-Saharan Africa. The greater numbers in North America reflect both high diversity and levels of threat in the Hawaiian Islands, California, and Florida, as well as extensive habitat modification, particularly for agriculture, and substantial efforts to identify species at risk of extinction. Lower numbers of endangered species in some regions reflect low species diversity due to severe environments and low human densities (Antarctica, Saharan Africa, and to a lesser extent Northern Asia).

Endangered species in the United States

Among the first countries to address the problems of endangered species seriously, the United States has listed 1264 species as threatened or endangered as of Feb-

ruary 2005 (USFWS 2005), and 1143 are on the Red List (IUCN 2004). In addition, more detailed data on the locations and status of at risk species, populations, and ecosystems has been collected on a state-by-state basis through Natural Heritage Programs (now expanded to include Canada and Latin America, and managed by NatureServe). The total list of at risk populations in the U.S. and Canada now includes over 15,500 occurrences (NatureServe 2005). Overall, a third of U.S. species are considered to be at risk of extinction (Stein et al. 2000), and the U.S. is second only to Ecuador in the number of species thought to be at risk of extinction globally (IUCN 2004).

Although a greater number of threatened species in the U.S. are plants (>5000), freshwater species (mussels, crayfish, stoneflies, and fishes) are threatened in higher proportions than any other group (Figure 3.8). Freshwater mussel species appear to be particularly diverse in the U.S., so the fact that 70% are imperiled is of global importance. Neither biodiversity nor the risk of extinction is distributed uniformly across the U.S. California is the state with the greatest species richness, as well as the greatest number of endemic species, but Hawaii has the greatest number of species at risk and the greatest number of species that have become extinct (Stein et al. 2002).

Using the expanded list of imperiled species existing in the natural heritage database as well as federally listed species as of 1996, Wilcove et al. (1998) classified threats for 1880 species and populations for which sufficient information was available. Over 85% of these were threatened by habitat degradation, while 49% were affected by invasive species, 24% by pollution, 17% by overexploitation and 3% by disease (Table 3.3). Vertebrates, freshwa-

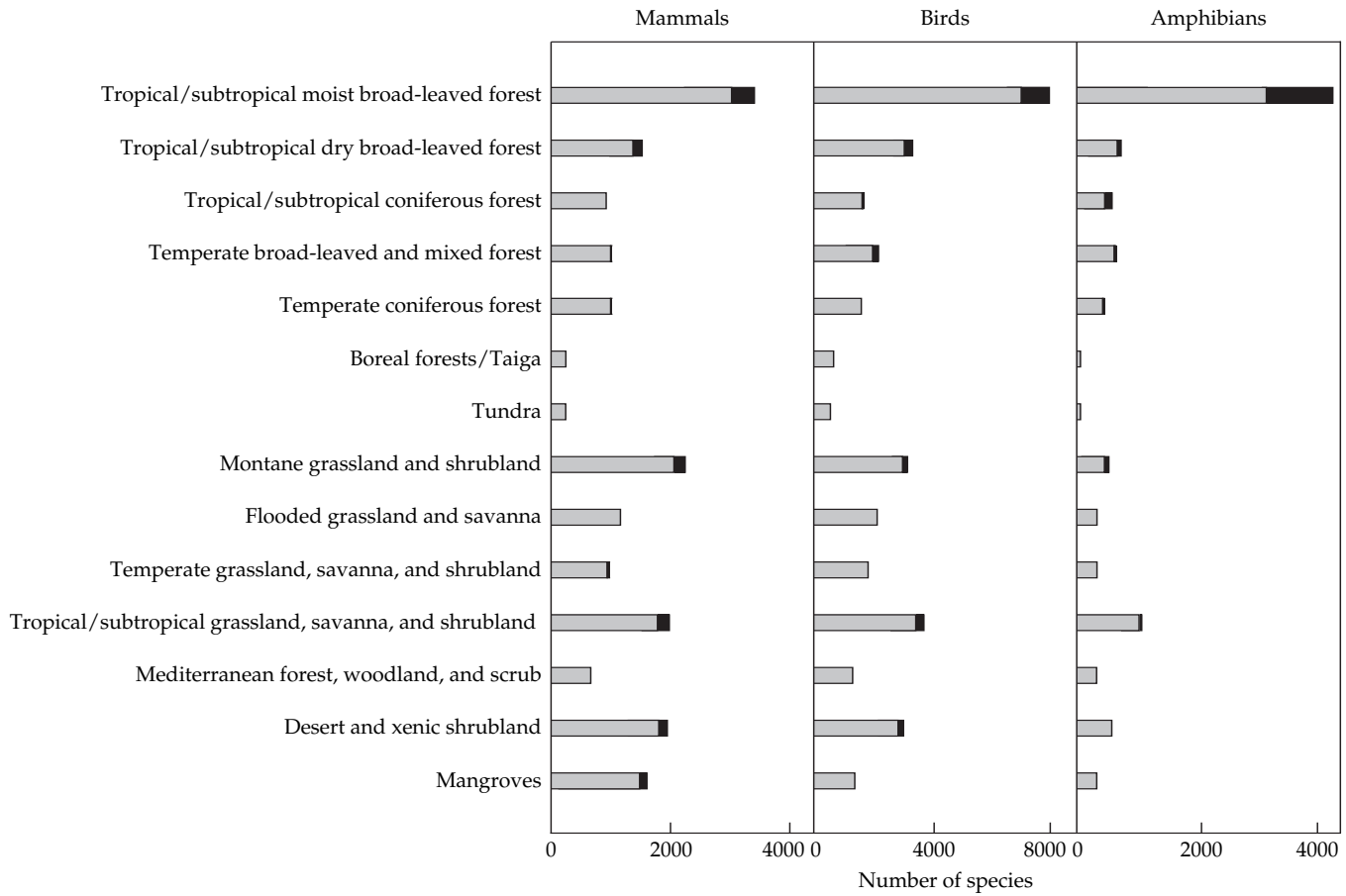


Figure 3.7 Species richness of mammal, bird, and amphibian species in the major biomes of the world. Black portions of the bars indicate number of threatened species. (Modified from Baillie et al. 2004.)

TABLE 3.3 Percent of U.S. Threatened and Endangered Species Affected by Five Types of Threat^a

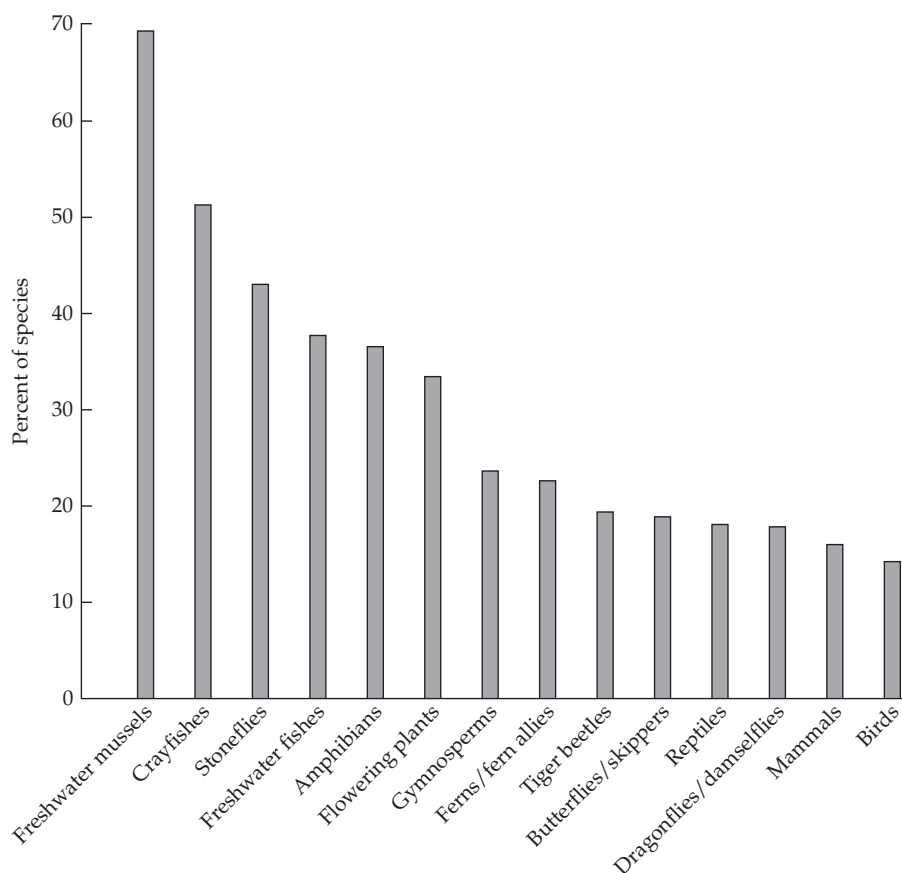
	Mammals	Birds	Reptiles	Amphibians	Fishes	Freshwater mussels	Crayfish	Other invertebrates	Plants
Threat	(85)	(98)	(35)	(60)	(213)	(102)	(67)	(143)	(1055)
Habitat loss and degradation	89	90	97	87	94	97	52	96	81
Overexploitation	45	33	66	17	13	15	0	43	10
Invasive species	27	69	37	27	53	17	4	46	57
Pollution	19	22	53	45	66	90	28	20	7
Disease	8	37	8	5	1	0	0	0	1

Note: Numbers in parentheses are the number of threatened species with threat data available.

Source: Wilcove et al. 1998.

^aListed by taxonomic group.

Figure 3.8 Proportion of species threatened with extinction by plant and animal groups in the United States. (From Stein et al. 2000.)



ter mussels, butterflies, and other invertebrates were threatened particularly by habitat destruction, while pollution and siltation impacts were most severe for aquatic species. Disease has limited distributions of many populations, and may have contributed to extinction of birds in the Hawaiian Islands (Van Riper et al. 1986). Invasive species pose threats to a greater proportion of plant and bird species in the Hawaiian Islands than in the continental U.S., and also to fish populations more than to other taxa.

Czech et al. (2000) examined the associations among 18 causes of endangerment for 877 species that were listed in the U.S. and Puerto Rico as of 1994. Urbanization was most frequently associated with other threats, as it involves both destruction of habitat directly and depletion of resources to support urban populations. Urbanization is also associated strongly with pollution, nonnative species, and the development of roads. Roads are not directly threatening to many species, but facilitate many forms of development that are threatening, such as urbanization, logging, industrial development, mining, and agriculture. Agricultural development was the most widespread threat, and associated most strongly with urbanization, reservoirs and pollution.

Threatened species in other countries

Although many countries maintain lists of threatened species, few have been analyzed in detail. Based on Red List data, Ecuador and the U.S. have the greatest number of endangered species (Table 3.4). Ecuador has a much higher number of listed plants than any other country. This has both a biological basis and a fortuitous one. Ecuador is a center of plant diversity where development, particularly in the Andean slopes has been extremely rapid recently, and thus a substantial fraction of evaluated plant species are threatened. Also, due to substantial efforts by concerned botanists, more than 2000 species have been evaluated—about half of those known from Ecuador. Such concerted efforts at reviewing threatened status have not been made for other centers of plant diversity, nor have they been undertaken for other taxa (for example, invertebrates) within the same country. Similarly, high numbers of species threatened in the U.S. reflects both true threat levels and much greater activity by its large cadre of biologists.

Although many countries do not harbor as long a list of globally threatened species, many have particularly high fractions of their species at risk. For example, over 80% of all plants and 30% of all vertebrates evaluated in

TABLE 3.4 *Numbers of Threatened Species (CR, EN, VU) in 12 Countries with the Greatest Overall Numbers of Red Listed Species*

	Mammals	Birds	Reptiles	Amphibians	Fishes	Invertebrates	Plants (%) ^a	Total
Ecuador	34	69	10	163	12	48	1815 (81)	2151
United States	40	71	27	50	154	561	240 (63)	1143
Malaysia	50	40	21	45	34	19	683 (60)	892
Indonesia	146	121	28	33	91	31	383 (60)	833
China	80	82	31	86	47	4	443 (73)	773
Mexico	72	57	21	190	106	41	261 (69)	748
Brazil	74	120	22	24 ^b	42	34	381 (68)	697
Australia	63	60	38	47	74	283	56 (33)	621
Colombia	39	86	15	208	23	0	222 (69)	593
India	85	79	25	66	28	23	246 (71)	552
Madagascar	49	34	18	55	66	32	276 (80)	530

Source: IUCN 2004 Red List Summary tables 5, 6a, and 6b.

^aPercent refers to the percent of those species evaluated that are threatened.

^bA complete revision of the list of threatened amphibians in Brazil has not been completed.

Madagascar are at risk of extinction. Madagascar has been subject to very high deforestation rates and other pressures, and also has a very high number of endemic organisms. Thus, the island nation is a focus of considerable conservation interest (Case Study 3.2).

Australia lists 1554 threatened species, the majority of which are vascular plants, followed by birds and mammals (Australian Government Department of Environment and Heritage 2005), while only 621 of these are also Red Listed and few of these are plants. Habitat degradation and invasive species are the most common factors in endangerment. Australia's landmass is roughly equal to that of the United States, but it has a very high degree of endemism, with roughly 85% of flowering plants, mammals, and freshwater fishes unique to this continent. Thus, most threatened species in Australia represent ones at risk globally.

Recently, Li and Wilcove (2005) summarized threats to vertebrates in China. Overexploitation is overwhelmingly the most important threat, contributing to endangerment of 78% of 437 species, and habitat degradation was also a pressing concern for 70% of these imperiled vertebrates (Figure 3.9). Nearly all endangered reptiles in China are overexploited for food and medicines. This is not surprising given the importance of traditional medicine for China's population, and strong dependence on wild species for protein (see Chapter 8). Pollution is a cause of endangerment in 20% of the cases, but as in other parts of the world, freshwater fishes are particularly susceptible with over 40% threatened by industrial pollutants and pesticides. Dams do not yet appear as a major problem, perhaps because they are still rela-

tively new and unstudied. Invasive species appear much less important, although this could be because they are little studied, or because global trade has a very long history and the species most vulnerable to invasives have already gone extinct (Li and Wilcove 2005).

Overall, understanding patterns of global endangerment, or even threatened status at a national level is fraught with uncertainty. These difficulties have led to some controversy concerning the relative rate of extinction currently compared with those occurring in geologic history (Box 3.3). Although, these issues are not entirely resolved, the consensus is that current rates of extinction already exceed "background" rates of extinction, and are at least approaching those of the mass extinctions.

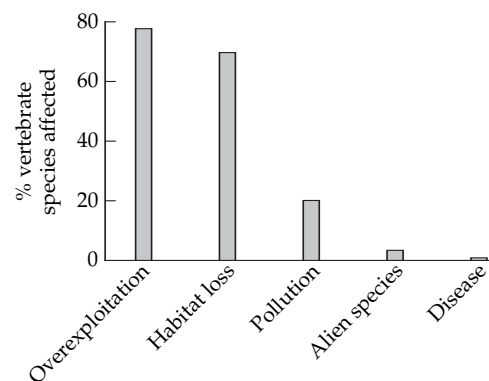


Figure 3.9 Contribution of major threats to endangerment among vertebrate species in China. (From Li and Wilcove 2005.)

BOX 3.3 Have We Set in Motion the Sixth Mass Extinction Event?

For a number of decades conservation biologists have called attention to the current rate of global extinction in extreme terms. Estimates of extinction rates vary, with most ranging from 50–10,000 times background extinction rates seen in the geologic record (Wilson 1992; May et al. 1995; Millenium Ecosystem Assessment 2005). To put our influences on biodiversity in context, many have tried to compare the current rate of extinction to the rates discernable from the fossil record. It is helpful to understand how these estimates are made, to provide the most defensible estimates for public discussion.

Before humans were dominant on Earth, the “background” rate of extinctions is estimated to have been about 0.1–10 species per year (May et al. 1995). During mass extinction events (see Figure 2.7), the rate of extinctions was 1–2 orders of magnitude higher (Raup 1994). Because neither the number of species on Earth during the mass extinctions is known (nor precisely how rapidly these extinctions may have occurred during a given 10,000–1,000,000 year interval), this estimate is highly imprecise, and thus difficult to compare with current estimates of extinction rates. Further, 95% of fossils are of marine invertebrates, while about 85% of extant species are terrestrial (May et al. 1995). How extinctions of marine invertebrates compared to extinctions in terrestrial and freshwater habitats is unknown.

Estimating current extinction rates is surprisingly difficult as well. This comes partly from the fact that it is much harder to prove that something does not exist, than that it does. To prove a species is extinct one needs to search exhaustively throughout a species’ range, during appropriate seasons, and sometimes for many years. The recent rediscovery of the Ivory-billed Woodpecker (*Campephilus principalis*; Fitzpatrick et al. 2005) long believed to be extinct, illustrates this difficulty. As this is obviously impossible to accomplish for all species on Earth, conservation biologists primarily use two methods to try to estimate current extinction rates.

First, we can derive extinction rate estimates from species-area curves. As described in Chapter 2, species richness increases with area. Species richness therefore also declines with decreases in area; thus as habitats are severely degraded, we can expect to see a concomitant loss of species. Conservation biologists thus use estimates of habitat change combined with those for species richness to project species losses (Figure A). The proportional reduction in species is then calculated as:

$$\Delta S = z \Delta A$$

where S is the number of species, z is the slope of the species–area curve for a given location, and A is the area of that location (May et al. 1995). The difficulty is that while increasingly we can estimate changes in forest cover with accuracy (ΔA), we do not know the relationship between extinction and reduction in area (z). We also don’t know the total number of species that may inhabit a given location, and thus we further extrapolate when we translate proportional reduction to an absolute number of losses per year. For example, tropical forest cover is being lost at a rate of 0.5%/year

(Achard et al. 2002), and if the value of z is 0.2 (as is commonly assumed), then we can expect to lose 0.125% of these species each year. If there are roughly 5 million species in tropical forests, then we are losing 5000 species per year. Of course, if the total number of species is smaller or larger, or z is higher or lower, we would get a different total (e.g., if $z = 0.15$ and only 1 million species exist in tropical forests, then the loss is 750 species per year). Despite the crudeness of these estimates, reasonable values of the parameters yield substantially more than 10 species per year (a high estimate of background extinction rates).

Second, extinction rate estimates are often based on numbers of directly observed extinctions (i.e., recorded in the IUCN Red List, or comparable national databases). The Red List documents 844 extinctions since 1500, a loss of 2.2% of all evaluated species and 0.04% of all described species. Certainly, this is an underestimate of global extinctions (and even more of local extinctions) because only a few taxa and locations have been documented well enough to allow a defini-

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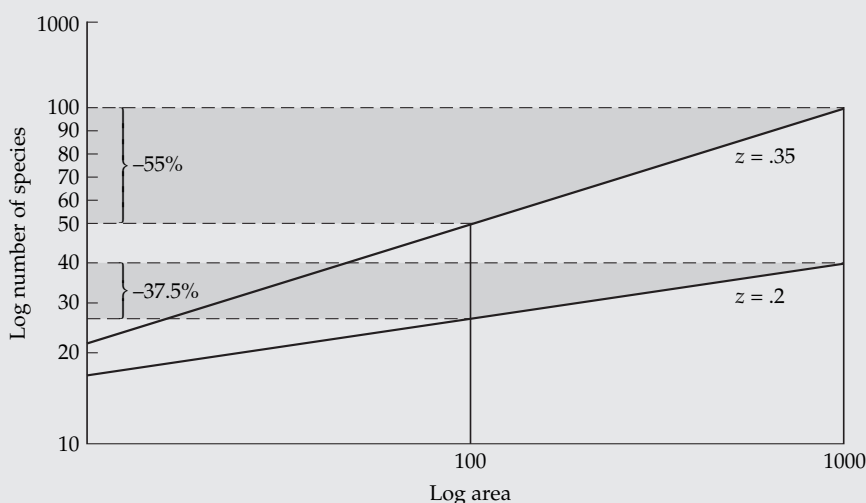


Figure A Species–area relationships based on the equation $S = cA^z$, with $c = 10$ and $z = 0.2$ or 0.35 . Note that a 90% decrease in area, from 1000 to 100 ha, would result in a predicted loss of 37.5% to 55% of the species, for a z value of 0.2 and 0.35 respectively. Greater z values (steeper species–area relationships) imply greater species losses per unit area. Most z values calculated from data fall between 0.15 and 0.35.

Box 3.3 *continued*

tive determination of extinction. Because we know the Red List total is too low, attempts are made to correct for this by extrapolating the rates for the best-known group to all species.

For example, roughly 100 birds and mammals have gone extinct between 1900 and 2000. To compare this to the fossil record, we need to calculate the loss as a percentage of all birds and mammals (currently 15,333 species). This translates to the loss of 0.65% of all birds and mammals each century, and 1 bird or mammal species per year. Average extinction rates of birds and mammals in the fossil record are on the

order of 0.003 species per year (McKinney 1997). Thus, the current extinction rate is 333 times greater than the background rate of extinction.

By these and related methods of estimation, we can conclude that the current rate of extinction already exceeds background rates of extinction, and either already or will soon equal or exceed those observed in the other five mass extinction events of Earth's history. Even losses less extreme than those seen in the mass extinction events are abnormal; a loss of 30% of the species on Earth is roughly equivalent to what occurs on average once in

10 million years (Raup 1994). Yet, more than 30% of amphibians, and over 40% of all species evaluated by the IUCN are threatened with extinction today.

Perhaps more important than the fact that species are going extinct at a great rate, should be the reflection that the time needed to recover levels of species diversity similar to those prior the extinction event is exceedingly long—e.g., 5–10 million years for coral reefs (Jablonski 1995). Our actions are causing biodiversity losses that cannot be recovered in our children's lifetime, or even that of our grandchildren or great grandchildren.

What Types of Species Are Most Vulnerable to Extinction?

Although we do not know the absolute rate of extinction of described and undescribed species today (see Box 3.3), we can describe with greater confidence which types of species are most likely to go extinct. Many attributes can make a species more vulnerable to extinction, including rarity, narrow habitat range, large area requirements, low reproductive rates, extreme specialization or coevolutionary dependencies. Further, species may be vulnerable to different threats, depending on their traits (Owens and Bennett 2000; Isaac and Cowlshaw 2004). Reviewing geological and historical patterns gives us insight into which species are most likely to go extinct in the future. Although a wide variety of possible factors may contribute to vulnerability for various species (see reviews by Ehrenfeld 1970; Terborgh 1974; McKinney 1997), most relate either to aspects of specialization or rarity.

Species vulnerability due to specialization

Many species, particularly in tropical moist forests, have evolved very narrow ranges of environmental tolerance and highly specialized diets or habits. Often these species are at particular risk because such ecological specialization lowers their resilience in the face of perturbations. Further, when these species are reliant on one or few other species, their existence will be threatened should these other populations decline or go extinct, as discussed earlier for the case of plant species dependent on one or few species of pollinators or seed dispersers.

Top carnivores, with low densities, large body size, high tropic position, and large area requirements are often cited as being particularly vulnerable to extinction, particularly

through habitat degradation, and also overexploitation (direct or indirectly of their prey) (Purvis et al. 2000). While this suite of factors certainly seems associated with greater extinction risk, large body size does not seem to have led to added risk for marine invertebrates (McKinney 1997), and other scientists have found stronger correlations between extinction risk and other life history traits, such as low rates of reproduction.

Because so many large-bodied species went extinct in the Pleistocene, it has long been assumed that large body size per se carries higher risks of extinction—in part because larger species were more valuable to hunters. While this has validity, close analysis reveals that extinction risk for Pleistocene megafauna was greatest for species with low reproductive rates, regardless of body size (Johnson 2002). Thus, what seems to have happened is that those species that could not replace themselves to meet the pace of human hunting went extinct. Further, nearly all large-bodied, slow-reproducing mammal species that survived to the present day were nocturnal, arboreal, alpine or deep-forest dwellers, suggesting that only those species that could elude human hunters survived to the present day (Johnson 2002).

Species with low reproductive rates typically can rely on adults to weather minor environmental variations, and thus have adapted to follow what is often called a “K-selected” life history strategy. These species are long lived, produce few young (which in some cases are cared for extensively by their parents), have high juvenile survivorship, and abandon reproduction when environmental conditions are poor to maintain high adult survivorship. Overall, these life history characteristics may make them unable to cope with the rapid changes occurring today. Because the evolutionary response to

stresses is to reduce reproduction, such species will decline in abundance, eventually to extinction.

Certainly, the decline and extinction of marine mammal species follows this pattern. Larger species were hunted initially, but these were also the species with the slowest maturity and lowest reproductive rates, and thus unable to replace themselves under industrial-scale exploitation (Roberts 2003). Many species of sharks, rays, and bony fishes today that have lower reproductive rates also show signs of greater vulnerability to exploitation, and thus greater extinction risks (Jennings et al. 1998; Dulvy et al. 2000). Often the most vulnerable species have later maturation, which also increases their susceptibility, as harvest before individuals have reproduced is thus more likely.

Vulnerability of rare species

A species may be rare for many reasons: because of a highly restricted geographic range, because of high habitat specificity, or because of low local population densities, as well as due to a combination of these characteristics (Rabinowitz et al. 1986; Gaston 1994; Table 3.5). Often a species may have attributes that seem to confer abundance, combined with ones that create rarity, and thus it is considered to be rare overall. For example, a species that occurs across an entire ocean basin (broad geographic range) and in high abundance, but is only found in a few isolated habitats such as deep-sea vents (high habitat specificity), is considered a rare marine species. Similarly, some species are never abundant anywhere, although their range may be quite extensive across broad geographic areas, as well as habitat types. Higher extinction rates are correlated particularly with species with re-

stricted ranges and low density (Jablonski 1991; Gaston 1994; Rosenzweig 1995; Purvis et al. 2000).

Species with highly restricted habitat preferences, such as a plant growing only within a rare soil type or seabirds that can only nest on cliffs with the correct prevailing winds, are particularly vulnerable to habitat degradation, as once their habitat is destroyed they are unable to adjust to another location. Common species that aggregate only in very particular locations, such as many bat species that roost in caves, are not only vulnerable to habitat degradation, but can be overexploited with ease. Often, recognizing habitat restrictions challenges us to transcend our experience to understand what environmental factors are critical to a marine invertebrate, an insect, or a fern.

Many of the highest estimates of future extinction rates are derived from our observations of extremely narrow ranges, or extreme endemism among many species in the tropics—particularly plants and insects, most of which are undescribed species (see Box 3.3). We rarely know why these species are so narrowly distributed, although many may be extreme habitat specialists or simply may not have dispersed to other places where they could persist, and thus have a restricted range for historical reasons. However, many analyses have shown that a restricted geographic range is the strongest predictor of extinction risk (e.g., carnivores and primates, Purvis et al. 2000; birds, Manne et al. 1999).

To better understand how extreme endemism can imperil species, consider an event documented in the mid-1980s. A group of scientists were doing RAP inventories in the western Andes of Ecuador, finding rapid turnover

TABLE 3.5 *Seven Forms of Species Rarity, Based on Three Distributional Traits*

		Geographic range			
		Large		Small	
Population size	Somewhere large	Common	Locally abundant over a large range in a specific habitat	Locally abundant in several habitats but restricted geographically	Locally abundant in a specific habitat but restricted geographically
	Everywhere small	Constantly sparse over a large range and in several habitats	Constantly sparse in a specific habitat but over a large range	Constantly sparse and geographically restricted in several habitats	Constantly sparse and geographically restricted in a specific habitat
		Broad	Restricted	Broad	Restricted
Habitat specificity					

of plant species, with large numbers of endemics. On a single ridge, Centinela, they found 90 endemic plant species. Just after their work was completed, the entire ridge was cleared for agriculture, and the 90 plant species were forever destroyed (Dodson and Gentry 1991). Although it is possible that some of these species may be found in other locations, many are likely now globally extinct, as well as the numerous associated animal species (especially insects) we can presume specialized on these endemic plants. In the words of E. O. Wilson (1992),

[Centinela] deserves to be synonymous with silent hemorrhaging of biological diversity. When the forest on the ridge was cut, a large number of rare species were extinguished. They went just like that, from full healthy populations to nothing, in a few months. Around the world such anonymous extinctions—call them “centinela extinctions”—are occurring, not open wounds for all to see and rush to stanch but unfelt internal events, leakages from vital tissue out of sight.

Island communities are typically rich in endemics, but also poorer in species than comparable mainland communities. Low species richness on islands is attributed to a combination of low colonization rates of new species (the functional equivalent of a low rate of speciation), and high extinction rates (because populations are usually small and subject to decimation by local catastrophes and stochastic variation) (MacArthur and Wilson 1967). Also, island communities have experienced extremely high extinction rates of species during recent centuries, primarily due to anthropogenic introductions of mammalian predators (mammals other than bats disperse poorly across ocean barriers) and mainland diseases.

Many groups are more endangered on island systems than on mainlands. In the new world, amphibians are much more endangered among the islands of the Caribbean (84% are at risk of extinction) compared with the adjacent continental landmasses of Mesoamerica (54%), South America (31%), and North America (21%; Young et al. 2004). As discussed earlier, avian extinctions have been much more common on islands, particularly due to combination of pressure from rapid habitat change, overexploitation, and invasive species that may act in an ecological role not represented on the island (e.g., introduced mammalian predators), and thus represent a challenge outside the evolutionary experience of many island species. However, carnivores and primates are no more likely to be endangered on islands than on continents (Purvis et al. 2000).

Small populations are generally more vulnerable to extinction than large ones. This has been seen in several comparisons of faunal surveys taken 50–100 years apart. Nearly 40% of small populations of birds (with less than 10 breeding pairs) went locally extinct in the California Channel Islands over an 80-year period compared with

only 10% of those populations with 10–100 pairs, only 1 population with 100–1000 pairs, and none of those with greater than 1000 pairs (Jones and Diamond 1976).

In the Baltic Sea, intense harvests of skates have caused the smallest populations to disappear, while larger ones are still extant (Dulvy et al. 2000). Many species with small populations may belong to species with large body size, which is often correlated with slower reproductive rates and other life history attributes that increase vulnerability to extinction.

Widely dispersed species that are always rare may be vulnerable to local extinction events, although they are less likely to become globally extinct. Some marine invertebrates may fall into this category, as well as populations of top carnivores. Although such species may not become globally extinct, local extinctions are potentially very damaging to communities and ecosystems, as discussed earlier.

We may need to worry most about **artificial rarity**, where a once widespread or abundant species has been reduced to a very small population size through human activities. Species that are artificially rare seem more likely to go extinct than species that are evolutionarily adapted to rarity (Kunin and Gaston 1997). Thus, small population size alone may be less predictive than a sudden reduction to small population size (which is one rationale for the criteria for listing species in the Red List; see Box 3.2).

“Bad luck”: Extrinsic causes of extinction due to human activities

In addition to these categories, we might also add one for species who simply have “bad luck” (Raup 1991). These species are not intrinsically vulnerable due to their traits, but rather have the misfortune to be in the wrong place at the wrong time, or of being particularly palatable to humans. That is, living in areas of greatest human impact, such as on arable soils, in river systems that are heavily used for commerce and subject to substantial pollution, or along coasts where human populations congregate, will thrust species that share those locations directly into harm’s way. For example, freshwater fishes in the most extensively altered ecosystems may all share an increased likelihood of extinction, despite having a wide variety of traits (Duncan and Lockwood 2001). Purvis et al. (2000) estimated that roughly half of the variation in extinction risk among carnivores and primates related to their exposure to anthropogenic disturbances, particularly to high rates of habitat loss or intense commercial or bushmeat exploitation.

Environmental changes may occur very rapidly, as they appear to have in the mass extinction events of geologic history, and then vulnerability to extinction may be widely shared among species (Raup 1991). The intensification of human pressures on ecosystems may have the same effect as the environmental changes of the past.

Our need to grow enough food to feed the increasing human population, particularly if large proportions eat meat, requires greater conversion of land for agriculture (see Chapter 6). Increasing rates of exploitation may hit those species with low reproductive rates hardest, but to some degree all species that are marketable may be endangered as local demand for bushmeat, for example, explodes with local human population density (see Case Study 8.3), or as commercial fisheries strive to meet world demand for protein (see Chapter 8). Global trade is increasing transport of species (see Chapter 9), and therefore increasing the chance that invasive species will take hold in some new place. Finally, our consumption of fossil fuels and other practices that drastically increase greenhouse gases has begun to change our climate (see Chapter 10)—which may be the worst luck of all.

An awareness of factors that enhance vulnerability to extinction can help us formulate plans to counteract these factors to some degree. Understanding which traits increase vulnerability also may help us predict which species will most need protections as human pressures increase in areas where they have been slight. However, it is also possible that increasingly species will best be categorized as simply having the bad luck to be in the path of human development.

Economic and social contexts of endangerment

Underlying threats caused by human development are powerful economic and social drivers. Perhaps most of all, economic growth and rising affluence do the most to increase the pace of habitat conversion, overexploitation of marine species for food, pollution of waterways, and transformation of our atmosphere that is changing our climate. In the U.S., causes of endangerment are those primarily associated with rapid economic growth—urbanization and agricultural expansion, infrastructure development (roads, reservoirs, wetland modification), and the byproducts of these activities (pollution, habitat degradation) (Czech et al. 2000). Moreover, geographic centers of endangerment currently occur where high diversity meets rapidly expanding economic activity in southern California, east-central Texas, and southern Florida (Dobson et al. 1997; Czech et al. 2000). As Czech et al. (2000) put it, “The list of endangered species is growing because the scale of the integrated economy, and therefore the causal network of species endangerment, is increasing.”

At the other end of the economic continuum, the majority of people struggle in poverty (UN Millennium Project 2005). Extreme poverty afflicts over 1 billion people, who live on less than \$1/day, are chronically hungry, lack clean water and sanitation, are burdened with preventable diseases, and often lack shelter and sufficient clothes. An additional 2.7 billion live on scarcely \$2/day, and are just able to meet their basic needs, but no more. Thus, it is

no wonder that unsustainable levels of burning, small-scale agriculture, grazing, and bushmeat hunting occur wherever these practices help the poorest people to survive. Biodiversity losses are clearly associated with this human tragedy, but even more serious are the signs that erosion of ecosystem services increasingly undercut the ability of human populations to escape extreme and moderate poverty (Millennium Ecosystem Assessment 2005).

Further, globalization spreads the dangers of economic expansion as countries prioritize international trade in natural resources to enhance their economies. This can exacerbate poverty where trade is not tied to sustainable practices that improve the lives of local people, but rather provide cheap goods that fuel the economies of developed nations. Often, pressures to overexploit and transform land come principally from decisions of large multinational corporations, and consumer demand in far-off countries. In addition, globalization also has radically accelerated the spread of nonnative species. Rapid economic expansion in China and other densely populated countries has raised concern that pressures on developing countries will intensify sharply in the near term (Millennium Ecosystem Assessment 2005).

Responses to the Biodiversity Crisis

Clearly, we live in a time of crisis for biodiversity. While many fine points can be debated, and some uncertainties remain, it is certain that humans have wrought radical change throughout the globe. Moreover, as our populations grow and consume more, ecosystems will continue to degrade, more species will go extinct, and human suffering on a staggering scale will continue. How can we respond to crises of this magnitude? Conservation biologists and promoters of human development agree that solutions will need to come from a mixture of (1) scientific analysis of and communication about the drivers of change in biodiversity and human welfare, (2) technological improvements, (3) legal and institutional instruments, (4) economic incentives and plans, and (5) social interventions. The mechanisms for achieving solutions will include preventative measures, such as establishment of protected areas (see Chapter 14), targeted interventions at genetic, species, and ecosystem levels that integrate ecological understanding with community-based problem solving (see Chapters 11–13), restoration of damaged ecosystems or endangered populations (see Chapter 15), and creation of truly sustainable forms of development (see Chapter 16).

Most approaches to conservation focus on species, ecological communities or ecosystems, or landscapes, although some also focus more broadly (and vaguely) on biodiversity overall (Redford et al. 2003). Because biodiversity conceptually spans the range from genes to ecosystems, and spatial scales from single ecological

communities to landscapes and larger, effective conservation is most likely to emerge from multiple approaches undertaken at a range of spatial scales, directed toward different conservation targets (species, ecosystems or landscapes). Conservation approaches focus from single species in a single site to all species across the globe, including species or ecosystem targets, and often explicitly including human communities and development (Redford et al. 2003).

Conservationists recognize that species approaches alone will not be sufficient to conserve biodiversity, and that actions on larger spatial scales targeting ecosystems and landscapes may be more efficient and effective as ecological processes will be more likely to remain intact when conservation is undertaken at these scales (Redford et al. 2003). However, conservation is usually achieved by many smaller actions, undertaken at smaller spatial scales. Overall, to address the numerous threats to biodiversity, conservationists need methods to prioritize conservation activities, and plans for how to achieve conservation at various scales. As Redford et al. (2003) put it, conservationists' generally are asking "where" questions to set geographical priorities, and "how" questions about developing and implementing strategies to conserve conservation targets at priority places.

The remainder of this section focuses on just two issues in promoting solutions—the use of national and international agreements to address our biodiversity crisis, and the issues involved in providing clear indicators of problems and of progress. The focus here will remain more on actions that are centered on species, whereas a discussion of approaches aimed more at habitat protection is included in Chapter 6, and longer treatments of approaches to solving the biodiversity crisis are included in Chapters 11–18.

Laws and international agreements that address biodiversity loss

Foremost among efforts to conserve biodiversity are national laws and international agreements that limit human impacts to threatened species and ecosystems, and establish a mandate for governmental and citizen action. Major international agreements, the landmark U.S. Endangered Species Act (ESA), and other key U.S. laws that protect biodiversity are described by Daniel Rohlf in Case Study 3.3. These institutional policy instruments are most effective when they reflect ecological and evolutionary understandings (as in the ESA, where protecting distinct population segments was given importance for future evolution and local community interaction), are well linked to human activities that can be amended, and have adequate enforcement

Many of the laws to protect biodiversity do so via lists of threatened species, as described earlier. In a broad

sense, these lists are used to set priorities for species protection, although of course many other factors—including economic and political ones—determine which species are targeted for conservation actions (Czech and Kaufman 2001). Laws and international agreements more effectively achieve conservation goals when they reduce the tendency for economic and political pressures to be paramount in decision-making, instead requiring a fair examination of potential harms and benefits to biodiversity. This may be accomplished via effective enforcement (e.g., the provision for citizen lawsuits in the ESA, or for severe trade restrictions to accompany failure to abide by animal trade prohibitions under CITES; see Case Study 3.3), and by mechanisms that promote economic incentives and disincentives (as are being developed under the Convention on Biological Diversity), or that increase public involvement in solution creation (e.g., Safe Harbor agreements under ESA).

Some conservationists have cautioned against using threatened species lists as too literal a guide for priorities. Because so many groups are poorly known, there is under-representation for many taxonomic groups (e.g., nearly all groups of invertebrates and nonvascular plants) and in areas of the world (most of the developing world, and most marine habitats). Prudence suggests we should be very cognizant that the biases in our knowledge could lead us to ignore taxa, or indeed other levels of biodiversity besides that of species that may be critical conservation targets (Possingham et al. 2000; Burgman 2002). Thus, often policies that are directed explicitly toward broader protections for habitat rather than species, or toward enhancing sustainable practices may be preferred to avoid such biases. However, usually conservation is not an either-or venture, but rather requires a suite of complementary approaches, some of which include admittedly imperfect policy instruments that motivate and guide action at many levels.

International agreements are meant to serve as motivators to action. At the 2002 Johannesburg World Summit on Sustainable Development, 190 countries committed to the reduction of biodiversity losses significantly by 2010. This in turn motivated efforts to develop more specific policies for conservation on global, national, and local levels. Further, this has motivated an examination of how we can track both problems and progress.

Identifying driving factors and trends in species endangerment

To create an effective plan to recover declining species, or to address biodiversity loss more broadly in some region of the world, a necessary step is to use rigorous scientific methods to determine which factors most influence population decline, and address our conservation actions to remove or ameliorate these threats (Caughley and Gunn

1996). While to some degree this is obvious, Caughley and Gunn found numerous examples where assumptions have led well-meaning conservationists astray. Deducing which causal factors drive declines should involve clearly delineating a plan of analysis to separate potential threats; this plan should include setting up testable hypotheses and predictions that follow from these hypotheses, and reviewing all evidence to evaluate each hypothesis carefully. To do this it is necessary to learn enough about the species' natural history to develop reasonable hypotheses. Commonly, the agent or agents of decline are not obvious, so conservation scientists have to become good detectives.

Beyond assessing the drivers of endangerment in particular cases, it is critical to track status trends to set priorities for intervention, and also to know when we are succeeding in protecting species. The IUCN has kept data on species endangerment for many years, and can now track the progress of the best-studied groups. The Red List Index (RLI) tallies changes in status due to either a deterioration or improvement of all threatened and near-threatened species since 1988 (Butchart et al. 2004). As applied to birds, RLI analyses show a portrait of steady deterioration of status (e.g., moving from vulnerable to endangered) (Figure 3.10). The RLI for birds has decreased by nearly 7% since 1988, roughly equivalent to 10% of all species in NT, VU, EN, and CR moving up into the next higher category of threat. For albatrosses and petrels the decline has been particularly steep, equivalent to a 25% drop in RLI since 1995, indicating a very perilous situation. A retrospective analysis for amphibians also indicates steep declines of roughly 15% in RLI (Baillie et al. 2004).

Most species groups are too poorly known to adequately evaluate trends, but a variety of indices help bridge this gap. These range from the index of biotic in-

tegrity that is used to assess stream health (Karr 1991), to composite indices that attempt to summarize global changes for the general public, business community, and government leaders. One of these composite indices, the Living Planet Index (LPI), summarizes change over time in populations of over 1100 terrestrial, freshwater, and marine vertebrate species (Loh et al. 2005). Because they are much better known, most of the data are drawn from bird and mammal species, on land in temperate climates. At present, these are the best data available, but it may be possible to weight the data to compensate for these biases as more data are collected on currently under-represented and little known groups (Loh et al. 2005). The LPI shows that terrestrial vertebrates have declined by 25% between 1970 and 2000 (Figure 3.11A). Further, freshwater species have declined more sharply than either terrestrial or marine vertebrates (see Figure 3.11B). Both these trends are disturbing. Importantly, the results of the LPI are discussed internationally, and are succeeding in conveying a straightforward and compelling message about overall trends.

Increasingly it is helpful to examine indicators of future change based on economic and social parameters (see also

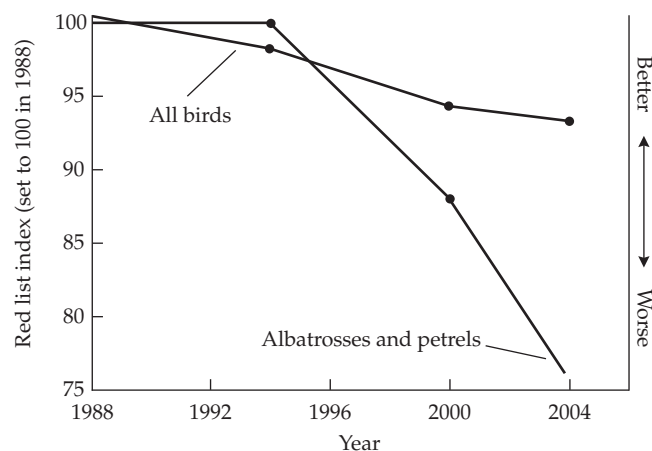


Figure 3.10 The Red List Index (RLI) shows a worsening of threatened status between 1988 and 2004 for all Red Listed bird species and a precipitous decline for albatrosses and petrels. (Modified from Butchart et al. 2004.)

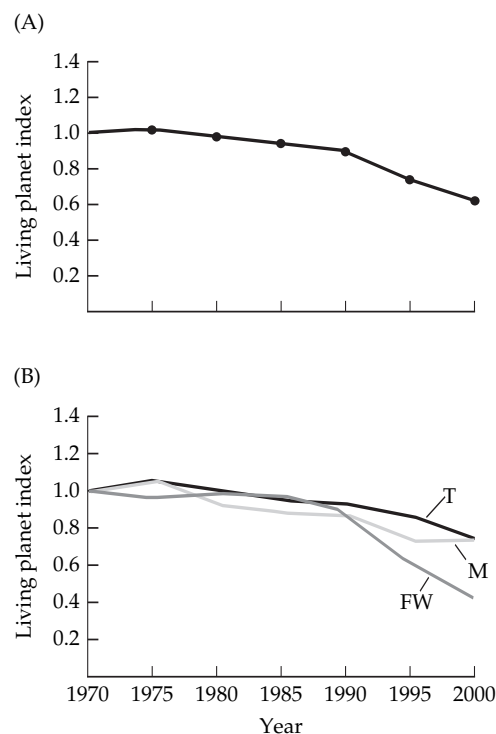


Figure 3.11 The Living Planet Index (LPI) tracks population trends for over 1100 terrestrial, freshwater, and marine vertebrates. (A) Terrestrial vertebrates have declined 25% from 1970 to 2000. (B) Freshwater (FW) vertebrates have declined more than either terrestrial (T) or marine (M) vertebrates. (Modified from Loh et al. 2005.)

Chapter 18). McKee et al. (2003) developed a stepwise regression model that predicted 87.9% of the variance in the density of threatened mammal and bird species based on human population densities and species richness in 114 countries. Because the model showed no bias, they used it to project potential impacts of increases in human population density on future levels of threat. If human populations grow as predicted by the United Nations and the correlations between human density and density of threatened mammals and birds do not change, then the number of threatened mammals and birds should increase by 7% by 2020 and by 14.7% by 2050 (McKee et al. 2003). While it does not direct specific action, the model can be used to help convince decision makers that interventions are needed now, and that delay has serious consequences.

The most comprehensive survey of the current status of biodiversity as it supports human life was made by a consortium of thousands of scientists in the Millennium Ecosystem Assessment (MA), completed in March 2005. Their conclusions are perhaps the most sobering of all. Although we have substantially increased food production worldwide, nearly all other indicators of ecosystem services have declined sharply since 1950, as human population grew from 2.5 to nearly 6.5 billion, and economic growth worldwide increased nine-fold (and in the U.S., twenty-five-fold). Threatening processes are ex-

pected to intensify, particularly habitat loss and degradation via pollution, species invasion, and climate change (Figure 3.12). Inland and coastal waters and grasslands have already borne the greatest impacts, and are expected to continue to be subject to intense pressures. The results of the MA should serve as a particularly strong wakeup call that, unless we wish to leave a substantially impoverished and dangerous world to our children, we need to make far-reaching changes in our global, national, and local behavior now.

To achieve our goals for conserving biodiversity, we will be well served by working to understand better the factors that drive human behavior, and the means that can effectively change destructive behaviors. Jeffrey Sachs, leader of the UN Millennium Development Project recently noted that the world's poorest people do not lack the *will* to follow more sustainable practices, but rather they and their governments lack the *means* (Sachs 2005). Human values, needs, and desires are powerfully, and quite imperfectly, translated into economic constructs that guide public policy and individual actions. One key to a long-term solution to the biodiversity and human poverty crises is to find ways to translate our ethics and the importance of biodiversity into our economics, and thus more integrally into our decision making.

Figure 3.12 Projected trends in threatening processes in different habitat types in the coming decades. Shading indicates the intensity of each process' impacts on biodiversity over the past century, with dark gray indicating the most impact and white the least. Straight upward arrows indicate very rapid increase in intensity of this threat at present; diagonally upward facing arrows indicate increases in the threat; sideways arrows indicate continuing levels of the threat; and downward facing arrows indicate declines in threat intensity. (Modified from Millennium Ecosystem Assessment 2005.)

		Habitat change	Pollution (nitrogen, phosphorus)	Over-exploitation	Invasive species	Climate change
Forest	Boreal	↗	↑	→	↗	↑
	Temperate	↘	↑	→	↑	↑
	Tropical	↑	↑	↗	↑	↑
Dryland	Temperate grassland	↗	↑	→	→	↑
	Mediterranean	↗	↑	→	↑	↑
	Tropical grassland and savanna	↗	↑	→	↑	↑
	Desert	→	↑	→	→	↑
Inland water		↑	↑	→	↑	↑
Coastal		↗	↑	↗	↗	↑
Marine		↑	↑	↗	→	↑
Island		→	↑	→	→	↑
Mountain		→	↑	→	→	↑
Polar		↗	↑	↗	→	↑

CASE STUDY 3.1

Enigmatic Declines and Disappearances of Amphibian Populations

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The First World Congress of Herpetology in 1989 and a National Research Council workshop in 1990 brought the accelerating losses of amphibian biodiversity to the forefront of conservation concerns. It long had been obvious that habitat destruction and alteration, introduction of nonnative species, pollution, and other human activities exact an increasingly heavy toll upon amphibians as well as on other taxa. By the time of these meetings, however, herpetologists realized that some of the declines and disappearances of amphibian populations and species were unusual in one respect: The causes of their loss were undetermined. These unexplained losses occurred in isolated areas relatively protected from most human impacts, particularly in montane regions in tropical/subtropical Australia, the western United States, Costa Rica, and other parts of Latin America. Especially noteworthy, detailed retrospective studies of declines in amphibians in large national parks in California (Drost and Fellers 1996; Fellers and Drost 1993) and in the Monteverde Cloud Forest Preserve in Costa Rica (Pounds et al., 1997) presented the first conclusive evidence of community-wide declines of amphibians.

Population declines and range contractions have continued. For example, during the latter 1990's 35 of 55 species disappeared from a study area in the Fortuna Forest Reserve in Panama (Lips 1999; Young et al. 2001). However, many of these

cases are complicated by the fact that not all sympatric amphibian species appeared to be affected.

A general problem with these reports was the lack of perspective, with a focus on what may be special cases. To rectify this situation, about 500 amphibian biologists were enlisted to participate in a Global Amphibian Assessment (GAA) conducted from 2000 to 2004 (Stuart et al. 2004). The assessment attempted to evaluate every species of amphibian across the planet, a challenging task when one considers the fact that the vast majority of species are tropical and most of these have been little studied. The GAA documented that the reports were representative of a widespread phenomenon, and that the problem is more acute than generally had been thought; 32.5% of the known species of amphibians are "globally threatened" (Figure A). The assessment also showed that community-wide amphibian declines were more likely to be encountered in the tropics. Many species showed no evidence of declines, however.

The causes of many documented declines and disappearances remain poorly understood despite a burgeoning literature on the subject. Nearly half of the 435 amphibian species classified as rapidly declining by the GAA are threatened primarily by "enigmatic" (unidentified) processes (Stuart et al. 2004). In this case study we briefly review the taxonomic and spatial patterns of these enigmatic losses and their major hypothesized causes. Although the enigmatic declines are our focus, well-documented threats such as habitat loss and overharvesting that are the primary cause of most losses of amphibian biodiversity (including over half of the rapid declines, Stuart et al. 2004) require attention as well.

Although amphibians are more threatened than some other groups, their plight is not unique (Gibbons et al. 2000). The case study of amphibian declines illustrates several themes applicable to studies of biodiversity losses in all taxa:

1. Biodiversity loss has many causes that are not mutually exclusive; several factors may act simultaneously on one population.

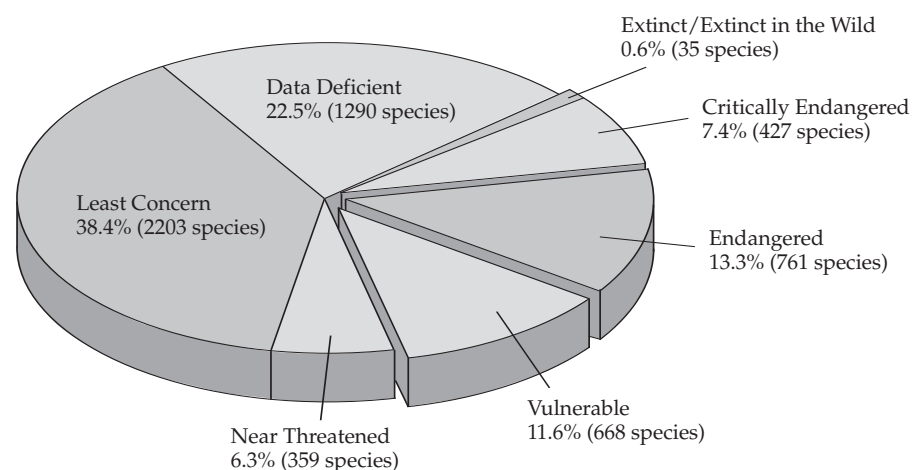


Figure A Over one-third of amphibian species have a threatened designation under the IUCN Red List. (From Global Amphibian Assessment 2004.)

2. Species, and populations within species, vary with respect to the importance of different threats.
3. The combined effect of several stressors can be worse than the sum of their individual effects. These synergistic interactions are especially difficult to study.
4. Experimental demonstration that a factor may affect a population is not proof that it is responsible for observed population declines.
5. No area on Earth is protected from human activities.

Species declining for enigmatic reasons are concentrated in the tropics, especially in Mesoamerica, the northern Andes, Puerto Rico, southern Brazil, and eastern Australia, although the phenomenon may be underestimated in poorly-monitored regions such as Africa (Stuart et al. 2004). Most species (82%) having unexplained declines are frogs and toads in the families Bufonidae, Hylidae, and Leptodactylidae. Ecologically, enigmatic declines are associated with species found in forests, streams, and tropical montane habitats (Stuart et al. 2004). A variety of hypotheses as to the underlying causes of these enigmatic declines have been proposed and studied by a host of conservation scientists.

Ultraviolet-B Radiation

Increased ultraviolet-B (UV-B) radiation is a possible explanation for declines and losses of amphibian populations in comparatively undisturbed areas. A large body of experimental evidence indicates that ambient levels of UV-B are harmful to some amphibian species at some locations, although effects may vary among populations, species, and geographic regions and with ecological factors such as elevation, water chemistry, and the presence of other stressors (reviewed by Blaustein and Kiesecker 2002; Blaustein et al. 2003a). For example, egg mortality in the western toad and Cascades frog was higher when eggs were exposed to ambient levels of sunlight in natural ponds in Oregon than when 100% of UV-B was blocked (Blaustein et al. 1994a; Kiesecker and Blaustein 1995). UV-B had no effect on the survival of Pacific treefrog eggs in the same experiments. The Pacific treefrog was found to have higher levels of an enzyme, photolyase, that facilitates the repair of DNA damaged by UV-B (Blaustein et al. 1994a). Ambient UV-B did not affect survival of western toad eggs in a field experiment conducted in Colorado (Corn 1998). Differences between the Oregon and Colorado results could be due to differences in genes, ecological conditions, or experimental design. UV-B had a greater effect on survival of long-toed salamander larvae from low-elevation populations than those from high-elevation populations under identical conditions in the lab (Belden and Blaustein 2002).

There is also much experimental evidence that UV-B has a greater effect on amphibians when combined with other stressors (Blaustein and Kiesecker 2002; Blaustein et al. 2003a). For example, UV-B decreased the survival of *Rana pipiens* eggs in acidic water but not at near-neutral pH (Long et al. 1995). In

some experiments western toad and Cascades frog eggs died as a result of UV-B increasing their susceptibility to a pathogenic fungus, *Saprolegnia* (Kiesecker and Blaustein 1995; Kiesecker et al. 2001a).

This body of experiments helps us understand some of the impacts of UV-B on amphibians, but does not show that UV-B is responsible for population declines and disappearances. It remains unknown whether the affected populations were exposed to increased UV-B, or that the effects of UV-B extend from individuals to the population level.

Ozone depletion is one factor that may have increased exposure of amphibians to UV-B, even in some locations at low latitudes (Middleton et al. 2001). Many other factors also affect the UV-B dose experienced by amphibians, including the attenuation of UV-B by water and by dissolved organic matter in water, breeding phenology, and behavior (e.g., Corn and Muths 2002, Palen et al. 2002). Climate warming and anthropogenic acidification may reduce concentrations of dissolved organic matter and thereby increase the depth to which UV-B penetrates aquatic habitats (Schindler et al. 1996; Yan et al. 1996).

Ecologists disagree on interpretation of research on the extent to which natural levels of dissolved organic matter currently protect amphibians from harmful levels of UV-B (Blaustein et al. 2004; Palen et al. 2004). Global climate change can affect precipitation, and consequently water depths and UV-B exposure (Kiesecker et al. 2001a). In dry years eggs will be closer to the surface of the water and thus more exposed to UV-B. A complicating factor is that in some regions, such as the Rocky Mountains, montane snow melt and amphibian breeding occur earlier in the season in dry years, when UV-B radiation is lower (Corn and Muths 2002). These issues illustrate why it is difficult to evaluate possible relationships between global climate change and UV-B exposure (Blaustein et al. 2004; Corn and Muths 2004). Integration of information on lethal and sublethal effects of UV-B throughout an amphibian's life cycle with demographic models will bring the phenomenon into a population dynamics framework (Biek et al. 2002; Vonesh and De la Cruz 2002).

Disease Pathogens

Pathogens may cause declines and disappearances of amphibian populations. There was little evidence for this hypothesis until a pathogen new to science, *Batrachochytrium dendrobatidis* (a chytrid fungus), was found in dead and dying frogs collected in the mid-1990's from declining populations in Australia and Panama (Berger et al. 1998; Longcore et al. 1999). *B. dendrobatidis* attacks only tissues that contain keratin, which include the mouthparts in anuran (frog and toad) tadpoles and the skin in salamanders and metamorphosed anurans (Berger et al. 1998; Bradley et al. 2002; Davidson et al. 2003). Research to date suggests that chytrid infections cause little or no mortality of anuran tadpoles or salamanders, although it can decrease the growth rates of the former, making them more susceptible to predators or other stressors (e.g., Davidson et al.

2003; Parris and Beaudoin 2004). *B. dendrobatidis* can kill metamorphosed frogs, either by producing a toxin or by interfering with skin functions such as respiration and osmoregulation (e.g., Berger et al. 1998; Rachowicz and Vredenburg 2004).

Batrachochytrium dendrobatidis has been isolated from other frog populations undergoing mass mortality events associated with population declines and disappearances, including *Rana yavapaiensis*, *R. chiricahuensis*, and *H. arenicolor* in Arizona (Bradley et al. 2002), the midwife toad (*Alytes obstetricans*) in Peñalara Natural Park, Spain (Bosch et al. 2001; Martinez-Solano et al. 2003b), and (retrospectively, using preserved specimens) several species in Las Tablas, Costa Rica (Lips et al. 2003a). It has also been isolated from populations not known to be in decline, including tiger salamanders in Arizona (Davidson et al. 2003), *Litoria wilcoxii* or *jungguy* (taxonomy uncertain) in Australia (Retallick et al. 2004), and *Xenopus laevis* in southern Africa (Weldon et al. 2004). Many individuals in these populations had light infections and appeared healthy. Antimicrobial peptides located in the skin may provide some species with natural defenses against *B. dendrobatidis* (Rollins-Smith et al. 2002a, b). Environmental conditions in some locations may not be favorable for the fungus. For example, *B. dendrobatidis* can grow and reproduce at temperatures of 4°C–25°C, whereas growth ceases at 28°C and 50% mortality occurs at 30°C (Piotrowski et al. 2004). This may explain why amphibian population declines and disappearances associated with chytrids have been observed in cool tropical montane areas (Berger et al. 1998; Lips et al. 2003a), but not in tropical lowlands where temperatures are often above 30°C.

Several scenarios for the association between chytrid fungus infection and population declines and disappearances are possible: (1) amphibians have long coexisted with *B. dendrobatidis*, and observed population changes are cyclical phenomenon that previous researchers may not have noticed; (2) amphibians have long coexisted with *B. dendrobatidis*, but environmental change or stress has made them more susceptible to the fungus or the fungus more pathogenic to the amphibian; and (3) *B. dendrobatidis* is a novel disease recently introduced to susceptible populations around the world through human activities such as the pet trade.

Scenario 1 would follow that of many wildlife diseases, including ranaviruses in North American tiger salamanders and in United Kingdom common frogs (Daszak et al. 2003). This scenario is considered unlikely for amphibian chytridiomycosis because of the large magnitude of the population changes and the lack of recovery in many cases (Daszak et al. 2003).

There are many ways in which an established coexistence between chytrids and amphibians may have changed over time, as in scenario 2. For example, increases in UV-B (Kiesecker and Blaustein 1995), exposure to pesticides (Taylor et al. 1999; Gilbertson et al. 2003), or other stresses can result in immunosuppression and disease emergence. Climate change can induce droughts, causing amphibians to aggregate around water bod-

ies and increasing their exposure to waterborne diseases such as *B. dendrobatidis* (Pounds et al. 1999; Burrowes et al. 2004). Immunosuppression would be likely to increase the prevalence of many diseases, however, not just chytridiomycosis.

Several pieces of data are consistent with the hypothesis that *B. dendrobatidis* is a novel pathogen that has recently been spread around the world with the assistance of humans. For four cases where *B. dendrobatidis* was associated with population declines and disappearances, chytrids could not be detected in museum samples collected prior to the population crash (Berger et al. 1998; Fellers et al. 2001; Lips et al. 2003a). Disease would have to have been very prevalent to allow detection from the small number of samples that were available, however (Lips et al. 2003a). Little genetic variation has been found so far in *B. dendrobatidis* collected around the world, although additional work is needed (Morehouse et al. 2003). Two amphibians that have been transported all over the world, the American bullfrog (*Rana catesbeiana*) and the African clawed frog (*Xenopus laevis*), are carriers of *B. dendrobatidis* (Daszak et al. 2004; Hanselmann et al. 2004; Weldon et al. 2004). The sudden, catastrophic nature of some declines and disappearances also suggests an introduced pathogen (Daszak et al. 2003).

If the chytrid is novel to most areas, where might it have originated? Some workers suggest it is endemic in populations of *Xenopus* in Africa (Weldon et al. 2004). The earliest documented case of chytridiomycosis was in a *X. laevis* collected in South Africa in 1938 (Weldon et al. 2004). The chytrid seems to have a benign relationship to this species, and *X. laevis* is a popular laboratory animal exported worldwide beginning with its use in pregnancy tests in the 1930s.

Introduced Species

Predation and competition from introduced species other than pathogens may have caused declines of some amphibian populations in isolated, seemingly protected areas. For example, the introduction of trout for sport-fishing is thought to have been an important factor in some disappearances of frogs in the Sierra Nevada of California. All but 20 of the 4131 mountain lakes of the state were fishless in the 1830s, as were most high-elevation streams in the Sierra (Knapp 1996). Stocking in Yosemite National Park reached a peak of a million fish each year in the 1930s and 1940s (Drost and Fellers 1996). Stocking has recently been reduced in the Sierra Nevada and discontinued in the region's national parks, in part because of concern about its effects on amphibians (Carey et al. 2003).

The best-documented effects of introduced fishes are for the mountain yellow-legged frog (*Rana muscosa*). It was once a common frog in high-elevation lakes, ponds, and streams of the Sierra Nevada (Grinnell and Storer 1924), but disappeared from over 85% of historical sites in the Sierra (Bradford et al. 1994b; Drost and Fellers 1996; Vredenburg 2004). *Rana muscosa* has a larval period of 1–4 years in the Sierra, and therefore requires permanent bodies of water, as do fishes (Wright and Wright 1949; Knapp and Matthews 2000). There is a strong

negative association between the presence of fish and of *R. muscosa*, even when habitat type and isolation are taken into account (e.g., Bradford 1989; Knapp and Matthews 2000). Densities of *R. muscosa* are low in the few sites where it does co-occur with fishes (Knapp and Matthews 2000; Knapp et al. 2001; Vredenburg 2004). *Rana muscosa* recolonizes lakes from which fishes have disappeared (Knapp et al. 2001) or have been removed experimentally (Vredenburg 2004; Figure B).

Although introduced fishes can account for the disappearance of *R. muscosa* from some sites, *R. muscosa* also disappeared from lakes without fishes in Sequoia, Kings Canyon, and Yosemite National Parks (Bradford 1991; Bradford et al. 1994b; Drost and Fellers 1996). Furthermore, some disappearances occurred during or after the late 1970s, after fish stocking was on the wane. One school of thought is that these other disappearances are an indirect result of fish introductions (Bradford 1991; Bradford et al. 1993; Knapp and Matthews 2000; Vredenburg 2004). According to this hypothesis, *R. muscosa* exists in metapopulations in which populations sometimes go extinct due to natural stochastic processes such as winterkill, drought, disease outbreaks, and predation. Sites are then recolonized by individuals migrating along streams. Stocking of fishes in lakes and streams has reduced the number, size, connectivity, and average habitat quality of *R. muscosa* populations, however. Thus, populations are now more likely to go extinct, and less likely to be recolonized if they do. The time lag between fish stocking and the disappearances of some populations is the

“extinction debt” predicted by metapopulation theory (Hanski 1998; Hanski and Ovaskainen 2002).

Introduced fishes and bullfrogs (*Rana catesbeiana*) are thought to have contributed to widespread range reductions of lowland yellow-legged frogs, *Rana boylei* (Hayes and Jennings 1986; Kupferberg 1997) and red-legged frogs, *Rana aurora* (Adams 2000; Hayes and Jennings 1986; Kiesecker et al. 2001b) in the western U.S. Their role is difficult to evaluate, however, because fish introductions, bullfrog introductions, and habitat alterations have occurred concomitantly across the landscape (Hayes and Jennings 1986). Several experiments have sought to disentangle these factors. Kupferberg (1997) found that bullfrog tadpoles outcompeted *R. boylei* tadpoles, and documented that breeding populations of *R. boylei* were greatly reduced in a stretch of stream that was unaltered except for the presence of *R. catesbeiana*. Experiments with *R. aurora* and native Pacific treefrog (*Pseudacris regilla*) tadpoles concluded that direct effects of the introduced species were less important than the widespread conversion of temporary ponds to permanent ponds, which provide better habitat for the introduced than the native species (Adams 2000). Kiesecker et al. (2001b) found that these habitat alterations intensified competition between *R. aurora* and *R. catesbeiana* tadpoles.

Negative relationships between the distribution of introduced fishes and the distribution and abundance of other amphibians have also been found, including the Pacific treefrog (*Pseudacris regilla*) in the Sierra Nevada (Matthews et al. 2001)

and most native species in the mountains of northern Spain (Brana et al. 1996; Martinez-Solano et al. 2003a). The effects of fishes on *P. regilla* and other species are apparently localized, perhaps because they use some habitats that fish cannot, such as ephemeral ponds and terrestrial areas, which may ameliorate landscape-level effects of fish stocking (Bradford 1989; Matthews et al. 2001). *Bufo boreas* and *B. canorus* frequently breed in fishless temporary ponds and produce toxins that fish avoid (Bradford 1989; Drost and Fellers 1996) and these fishes may have little affected their declines. Because fishes have been introduced into nearly all montane systems on the planet, the possibility of impacts exists for many amphibian species, most of which are as yet unstudied.

Chemical Pollutants

Pesticides, herbicides, heavy metals, and other chemical pollutants can have lethal, sublethal, and indirect effects on all organisms, including amphibians (Sparling et al. 2000; Blaustein et al. 2003a; Linder et al. 2003). Chemical pollution might seem to be a minor threat in isolated, protected areas; however, chemical contaminants may be transported long distances through at-

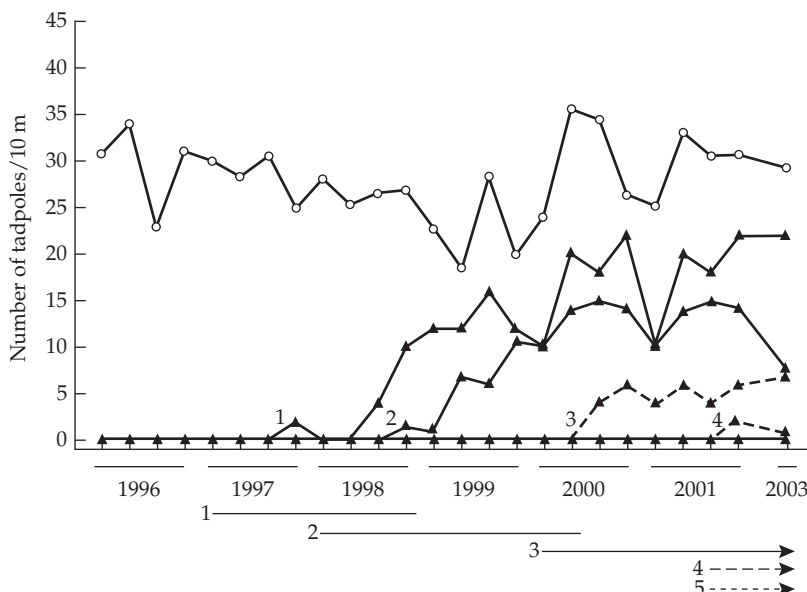


Figure B Density of larval *Rana muscosa* in 21 lakes in the Sierra Nevada, California, from 1996 to 2003. Filled triangles represent trout removal lakes ($n = 5$), and numbers correspond to individual lakes. Open circles indicate fishless control lakes ($n = 8$). The horizontal bars beneath the graph indicate the time period over which trout were removed. *R. muscosa* had not yet recolonized lake 5 after trout were removed in 2001. Control lakes with trout ($n = 8$) never had any frogs present during the duration of the study. No tadpole counts were made in 2002. (Modified from Vredenburg 2004.)

mospheric processes. Further, extremely low, supposedly safe doses of chemicals can harm biota (e.g., Marco et al. 1999; Reilyea and Mills 2001). For example, exposure to 0.1 ppb of the herbicide atrazine causes gonadal deformities in northern leopard frogs (*Rana pipiens*) and African clawed frogs (*Xenopus laevis*), whereas the U.S. drinking water standard for atrazine is 3 ppb (Hayes et al. 2003, Hayes 2004).

The best-documented connection between long-distance transport of chemical pollutants and enigmatic changes in amphibian populations is in California. Prevailing winds transport pesticides and other contaminants from areas of intensive agriculture in the Central Valley to national parks, forests, and wilderness areas in the Sierra Nevada (Fellers et al. 2004; LeNoir et al. 1999; Sparling et al. 2001). Disappearances of *Rana aurora draytonii*, *R. boylei*, *R. cascadae*, and *R. muscosa* populations in California are correlated with the amount of agricultural land use and pesticide use upwind (Davidson et al. 2001; Davidson 2004). *Rana muscosa* that were translocated to an area of Sequoia National Park from which they had disappeared (despite the absence of fish) developed higher tissue concentrations of chlordanes and a DDT metabolite than were found in persisting *R. muscosa* populations 30 km away (Fellers et al. 2004).

These studies provide correlative evidence that pesticides contributed to declines and disappearances of amphibian populations in the Sierra Nevada. Acceptance of this hypothesis will require additional evidence connecting the presence of pesticides and their effects on individuals to effects on populations. This connection cannot be assumed. For example, leopard frogs remain abundant in many areas highly contaminated with atrazine in spite of this herbicide's negative effects on reproductive organs (Hayes et al. 2003). Interactions between pesticides transported long distances and other factors have been suggested as a cause of amphibian declines and disappearances in other protected areas, including Monteverde and Las Tablas, Costa Rica (Pounds and Crump 1994; Lips 1998) and The Reserva Forestal Fortuna, Panama (Lips 1999), but remain little investigated at these sites.

Acid rain is another type of pollution that could affect amphibian populations in isolated areas (Harte and Hoffman

1989). Chemical analyses of water samples in several regions, however, suggested that acid precipitation is an unlikely causal factor (e.g., Richards et al. 1993, Bradford et al. 1994a, Vertucci and Corn 1996).

Natural Population Fluctuations

Population sizes of amphibians, like those of many other taxa, may fluctuate widely due to natural causes. Drought, predation, and other natural factors may even cause local extinctions, necessitating recolonization from other sites. Some declines and disappearances of amphibian populations in areas little affected by humans may be natural occurrences from which the populations may eventually recover, provided that source populations exist elsewhere in the general area (Blaustein et al. 1994b; Pechmann and Wilbur 1994). Natural processes may account for declines and extinctions in the Atlantic forest of Brazil (severe frost and drought, Heyer et al. 1988; Weygoldt 1989), and the loss of some montane populations of the northern leopard frog in Colorado (drought and demographic stochasticity, Corn and Fogleman 1984). Natural fluctuations may also interact with human impacts, resulting in losses from which recovery is unlikely.

Pechmann et al. (1991) used 12 years of census data for amphibians breeding at a pond in South Carolina to illustrate how extreme natural fluctuations may be, and how difficult it can be to distinguish them from declines due to human activities (Figure C). Even "long-term" ecological studies rarely capture the full range of variability in population sizes (Blaustein et al. 1994b; Pechmann and Wilbur 1994). Formulating "null models" of the expected distribution of trends in amphibian populations around the world, against which recent losses may be compared, is a challenging task (see Pechmann 2003 for a review). For example, populations in which juvenile recruitment is more variable than adult survival may decrease more often than they increase, because the average increase is larger than the average decrease (Alford and Richards 1999). The expectation for these populations is that more than half will exhibit a decline over any given time interval even if there is no true overall trend.

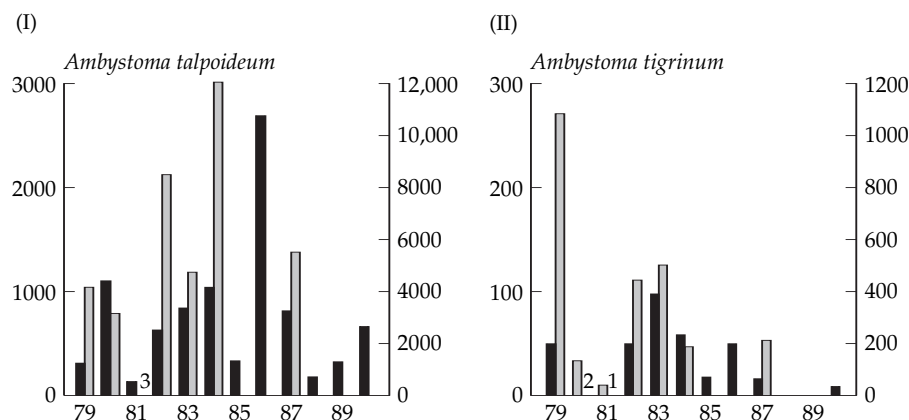


Figure C Natural fluctuations in population size of two species of salamanders in a temporary pond, Rainbow Bay, South Carolina from 1979 to 1990. Numbers of both breeding females (black bars, left axis) and metamorphosing juveniles (gray bars, right axis) vary greatly annually, and some species disappear from and reappear in the system. Numbers in the figure refer to extremely low counts of 3 or fewer individuals. Such species may be poor choices as indicators for the larger system since their natural population fluctuations are so large. (From Pechmann et al. 1991.)

Climate Change

Changes in amphibian population sizes and distributions are often related to changes in environmental temperatures and precipitation (e.g., Bannikov 1948; Bragg 1960; Semlitsch et al. 1996). This variation has traditionally been viewed as natural (Pechmann and Wilbur 1994). The effects of anthropogenic greenhouse gas increases on global climates suggest alternative interpretations in some cases, however.

Some of these alternatives are mediated by the possible effects of greenhouse warming on the El Niño/Southern Oscillation (ENSO), a cyclical warming (El Niño) and cooling (La Niña) of the eastern tropical Pacific. Kiesecker et al. (2001a) found that during El Niño events, precipitation in the Oregon Cascade Mountains was low, resulting in low water levels at *Bufo boreas* breeding sites. The shallow water afforded toad eggs little protection from UV-B radiation, which increased their vulnerability to a pathogenic fungus (*Saprolegnia ferax*), causing high mortality. Kiesecker et al. (2001a) hypothesized that if global warming is increasing the intensity and frequency of El Niño conditions, this may result in amphibian population declines via scenarios analogous to that elucidated by their research with western toads. The effects of global warming on El Niño conditions remain unresolved, however (Cane 2005; Cobb et al. 2003, see Chapter 10).

The disappearance of the golden toad (*Bufo periglenes*) and other frogs from the Monteverde Cloud Forest Preserve in Costa Rica in the late 1980s was associated with an El Niño event, as were subsequent cyclical reductions of some remaining amphibian populations (Pounds et al. 1999). During El Niños, the height at which clouds form increases at Monteverde, reducing the deposition of mist and cloud water that is critical to the cloud forest during the dry season. Pounds et al. (1999) suggested that greenhouse warming has exacerbated this El Niño effect (see Case Study 10.3), citing a global climate model simulation that predicted warming will increase cloud heights at Monteverde during the dry season (Still et al. 1999). This model represents only a crude proxy, because its spatial resolution is too coarse to explicitly model cloud formation on a particular mountain (Lawton et al. 2001; Still et al. 1999). Regional atmospheric simulations and satellite imagery suggest that lowland deforestation upwind also may have increased cloud base heights at Monteverde (Lawton et al. 2001).

Atelopus ignescens and several other *Atelopus* species are thought to have disappeared from the Andes of Ecuador during 1987–1988, which included the most extreme combination of dry and warm conditions in 90 years (Ron et al. 2003). Temperatures in this region increased 2°C over the last century, probably largely due to greenhouse warming (Ron et al. 2003). Other studies also have detected associations between enigmatic declines and disappearances of amphibian populations and temperature and precipitation anomalies (Laurance 1996; Alexander and Eischeid 2001; Burrowes et al. 2004). In these cases the anomalies were within the range of natural variation, thus it is unlikely that they were the direct cause of the amphibian losses, although they may have been a contributing factor. Global

warming has been associated with earlier breeding of some amphibian species (e.g., Beebe 1995; Gibbs and Breisch 2001). Although these phenological changes could potentially result in demographic or distributional changes, there is no evidence that they have to date, except when earlier breeding is associated with dry conditions as for western toads in Oregon (Blaustein et al. 2003b, see also Corn 2003; Kiesecker et al. 2001a).

Subtle Habitat Changes

Subtle habitat changes are an understudied potential cause of enigmatic losses of amphibians. For example, fire suppression in Lassen Volcanic National Park, California, has allowed encroachment of trees and shrubs in and around open meadow ponds, streams, and marshes, rendering these sites unsuitable for *Rana cascadae* breeding (Fellers and Drost 1993). Pond canopy closure is known to have local effects on amphibian biodiversity elsewhere (Halverson et al. 2003; Skelly et al. 1999). Construction of dams in the Sierra Nevada has altered temperatures and hydrological regimes downstream, making the habitat unacceptable for *Rana boylei* breeding (Jennings 1996).

Conclusions

The current thinking of the majority of researchers is that there are many interacting causes for enigmatic amphibian losses. Great challenges face those studying declining amphibian populations in scaling individual effects to the population level. Further challenges include directly testing hypotheses formulated from correlative studies with well-designed field experiments to elucidate those mechanisms that are driving the perceived patterns of decline. Synergistic studies can start by dealing with individual phenomena such as the effects of introduced species, and from this foundation scale up to include multiple factors.

Meanwhile, is there nothing we can do to combat these declines? Not at all. A good example is the rapid rebound of *Rana muscosa* populations following trout removal in the high Sierra Nevada (Vredenburg 2004; see Figure B). Management changes are most likely to be put into effect when direct evidence of the phenomenon has been demonstrated, as has been the case in large national parks in California where fish removal is being actively pursued. Even though fish do not explain all of the declines detected, removal of fishes nonetheless has a salutary effect.

A greater challenge is the infectious disease problem, especially chytridiomycosis. Whereas adult *Rana muscosa* with chytridiomycosis in the laboratory invariably die, field studies have shown that some infected adults can survive the summer (at a minimum) under certain circumstances in the field (Briggs et al. 2005). Models indicate that survival of at least some fraction of infected post-metamorphic individuals is crucial to the persistence of populations (Briggs et al. 2005), and studies in progress should help us understand what factors are associated with survival of infected individuals in this and other species. Achieving a balance between scientific understanding of problems and conservation action is a continuous challenge.

CASE STUDY 3.2

Hope for a Hotspot

Preventing an Extinction Crisis in Madagascar

Carly Vynne, University of Washington and Frank Hawkins, Conservation International

Madagascar as a Biodiversity Hotspot

The island nation of Madagascar is world-renowned for its high levels of endemism and biodiversity richness. Despite its proximity to the African mainland, Madagascar does not share any of the typical African animal groups such as elephants, antelopes, or monkeys. Its 160 million year separation has instead resulted in a unique assemblage of plants and animals. Madagascar is characterized by tropical rainforest in the east, dry deciduous forests in the west, and a spiny desert in the far south.

The Madagascar and Indian Ocean Islands Hotspot, which includes the neighboring islands of the Mascarenes, Comoros, and Seychelles, has an impressive 24 endemic families, thus making it one of the highest-priority biodiversity hotspots on earth. At the species level, 93% of mammals, 58% of birds, 96% of reptiles, and 99% of the amphibians are endemic (Figure A). All 651 terrestrial snails and 90% of the estimated 13,000–15,000 plant species are endemic (Mittermeier et al. 2004). In the last 15

years, thousands of new plant species have been identified, as well as many new animal species (22 mammal, 40 fish, 40 butterfly, 150 reptile and amphibian, and 800 ant species). Certainly, many new species remain to be discovered and described.

Hotspot under Siege

Madagascar stands out as one of the highest global priorities for conservation not only because of its high biodiversity values, but also because of the grave threats facing the country. It is estimated that 83% of the primary forest cover of Madagascar has already been lost. The percentage is even higher for the hotspot's smaller islands, and only 10% of the original 600,461 square kilometers of natural habitat remain throughout the entire hotspot. Should current rates of forest destruction continue, all of Madagascar's forests would be lost within 40 years.

The current human population of between 17 and 18 million is growing at about 2.8% per year, doubling every 20 to 25 years. This population is mostly rural, and extremely poor; the per capita annual income in 2002 was U.S.\$268. Currently about 2.4 million people live within 10 km of protected areas.

Due to its geographic isolation, humans only arrived on Madagascar about 2000 years ago. The Malagasy people, who are of both African and Asian descent, brought with them agricultural methods such as slash and burn agriculture and extensive cattle grazing on pasture that needs to be burned regularly. These land uses have been particularly detrimental because of infertile soils and low-life resistance of native vegetation. *Tavy*, the traditional slash and burn method of clearing rainforest for rain-fed rice production, continues to be a primary threat today, with around 1%–2% of forest being lost annually to this cause.

The disappearance of forest cover has reduced soil fertility and increased erosion, and poses a dire threat to biodiversity. Estimates show that Madagascar loses the equivalent of 5% to 15% of its gross domestic product annually through declines in soil productivity, loss of forests, and damage to infrastructure linked to forest destruction. The high central plateau of Madagascar has been essentially deforested, and soils washed into the sea are visible from space, giving Madagascar the appearance of having a "red ring" around the island.

Subsistence fuel wood collection, charcoal production, and hunting, also affect Madagascar's forests. Wildlife trade has a serious impact on some endemic amphibians, reptiles, and succulent plants. The proliferation of invasive species affects some ecosystems and species diversity, particularly in aquatic areas. For example, *Bedotia tricolor*, a native endemic fish, is



Figure A Madagascar is home to an enormous number of endemic species, including this panther chameleon (*Furcifer pardalis*). (Photograph by F. Hawkins.)

now listed as Critically Endangered due in part to competition from an introduced predator, the spotted snakehead fish (Loiselle et al. 2004).

Impacts of commercial timber exploitation are greater than in some parts of the tropics, as trees are generally smaller and compete poorly with introduced species. Regeneration of primary rain forest after logging and slash-and-burn consists mostly of introduced species. Presence of invasive species is not a temporary state; rather, invasive species dramatically alter the trajectory of forest succession (Brown and Gurevitch 2004).

With such human pressures, the resultant threats to biodiversity are not surprising. Currently, 283 birds, mammals, and amphibians are globally threatened with extinction. Of these, all but two are endemic. To help thwart a major extinction spasm from one of the most biologically rich places on Earth, a substantial effort in conservation is currently underway.

Promise for Protected Area Expansion

At the 2003 World Parks Congress held in Durban, South Africa, the President of Madagascar, Marc Ravalomanana, announced the Durban Vision—the Government of Madagascar's commitment to increase protected areas. In his words, "We can no longer afford to let one single hectare of forest go up in smoke or let our many lakes, marshes and wetlands dry up, nor can we inconsiderately exhaust our marine resources. I would like to inform you of our resolve to bring the protected areas from 1.7 million hectares to 6 million hectares over the next five years. This expansion will take place through strengthening of the present national network and implementation of new mechanisms for establishment of new conservation areas."

Prior to this announcement, only 2.4% of the hotspot is designated under the most highly protected categories I–IV of IUCN protected areas; overall only 3% of the land area has any protection. The President of Madagascar pledged to seek \$50 million from the international community to make the protected area expansion a reality, and within six months \$18 million had been pledged to the trust fund.

Maximizing Protected Area Design for Biodiversity Conservation

To ensure that investments in Madagascar's protected areas provide the highest possible coverage of species diversity, many conservation organizations and independent researchers are working to assemble scientific data that will highlight areas most urgently in need of protection.

New databases make systematic planning for a network of protected areas possible. First, geographically associated, digital GIS files of Madagascar's protected areas were developed in preparation for the World Parks Congress. From these maps it is possible to identify "gaps" where important areas remain without park protection (see Essay 14.2). Second, distribution maps now exist for many of Madagascar's threatened species. A third important dataset is a forest cover change map. A map of deforestation between 1950 and 2000 is shown in Figure B. From this dataset and map, planners may see areas that are undergoing rapid habitat conversion and areas where suitable habitat patches remain for protection in reserves. In addition it can be used to evaluate specific threats to species that occupy small ranges or limited habitats.

The Durban Vision has spurred conservation biologists and planners to take a countrywide view and use emerging information both to develop tools that can help guide decision mak-

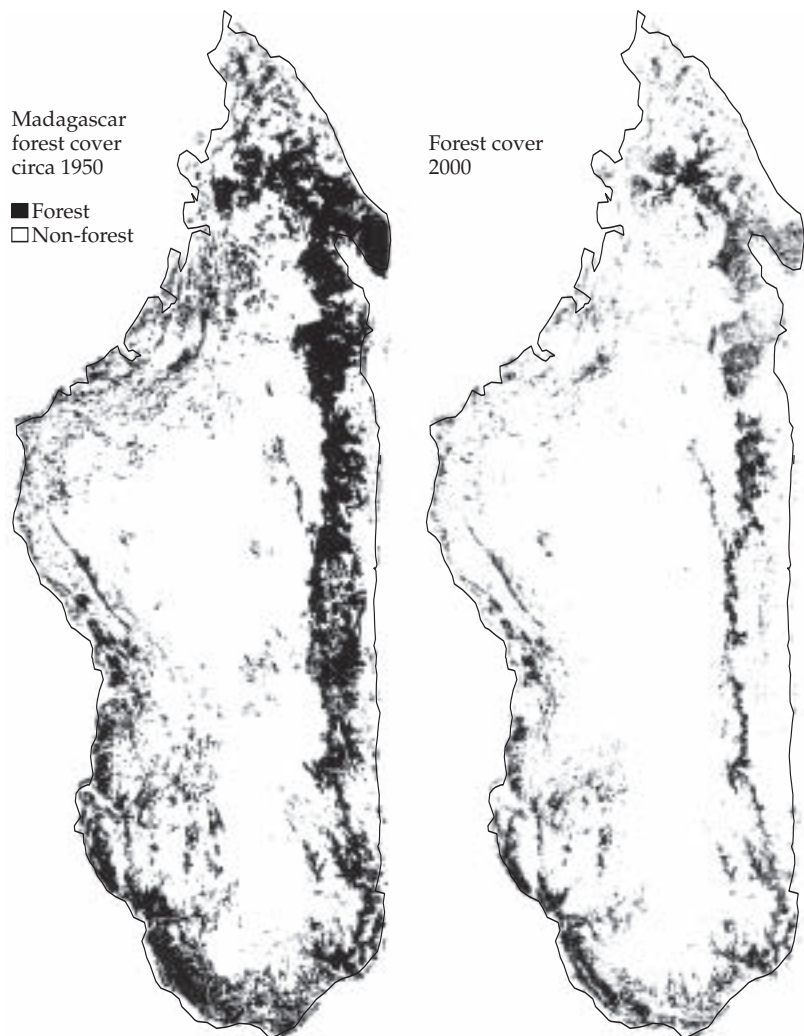


Figure B Loss of forest cover on Madagascar between 1950 and 2000. (Cartography by M. Denil © Conservation International.)

ing and to define key biodiversity areas. Not only will these processes be used to optimize expansion of the protected area network, but the information can help inform assignment of management categories so that the highest priority areas are afforded the greatest protection.

From Planning to Park Establishment: The Case of Masoala

Even with the emerging tools now available for reserve selection, seldom are protected areas implemented based on scientific design principles. A notable exception to this is Masoala National Park, established in Madagascar in 1997. The establishment of this park created Madagascar's largest protected area. The planning process was based on biological and socioeconomic principles of conservation design. There is much to learn from the Masoala design phase to ensure creation of successful reserves in the future.

The Masoala Peninsula of northeast Madagascar is one of the largest forest blocks in the country. Beginning in 1990, efforts were underway to establish an integrated conservation and development project (ICDP), as well as a protected area, on the peninsula. As local use of the ICDP was part of the strategy, an important component of park design was to demarcate core forest areas for biodiversity conservation. Thus, design criteria emphasized that the park be of sufficient size to buffer against disturbances and protect its resources. The second component of the design aimed to enable socioeconomic sustainability and prevent conflicts with local communities (Kremen et al. 1999).

To design the park, maps of different forest types were compiled. Next, a biological inventory was completed, with surveys for birds, primates, small mammals, butterflies, and cicindelid and scarab beetles along five environmental gradients. These data were used to ensure as many species as possible were represented in the core area of the park. To incorporate socioeconomic data, all villages and settlements on the peninsula were mapped and focus-group interviews were held to obtain socioeconomic and agricultural data. Kremen and colleagues subsequently conducted an economic use analysis to determine where to zone for selective logging. Within the use zone, a forest inventory assessed timber resources. Finally, a threats analysis identified and ranked the major threats to biodiversity and identified areas likely to be lost without increased levels of protection.

The full range of elevation gradients present on the peninsula were required if the park was to meet the objective of protecting all known biodiversity. The peripheral, threatened zone in the park's eastern limit had a high edge-to-area ratio and would have been extremely difficult to protect. Thus, this area was left outside of the park to serve as an ecological buffer and an economic support zone for local people. The economic analyses suggested that sustainable forest management in this zone would provide better returns to local communities than slash-and-burn practices.

The recommended design led to the establishment of the present day Masoala National Park, which is 2300 km² and is

surrounded by a 1000 km² buffer of community managed forest (Kremen et al. 2000). Slash-and-burn farming for subsistence rice production is the principal threat to unprotected forests. Thus, the park management is working with local communities to create economic incentives for maintaining the boundary forest. Continued assistance to the local communities will be required over a long time period.

That Masoala exists as a national park today should be credited not only to sound design, but also to persistent and persuasive pressure from NGOs. As described by Kremen et al. (2000), "Several timber companies were prospecting for concessions on the Masoala Peninsula during the time that the National Park was being established, and the government nearly abandoned the park project in favor of a logging company. The conservation and diplomatic community played a large role in persuading the government to reject the logging companies' proposals, using both political and economic arguments. Without this pressure, the Masoala Peninsula, one of Madagascar's most important reservoirs of biodiversity, would perhaps have become a forestry concession instead of a national park."

Continuing the Legacy: Sustainability and Financing of a New Reserve System

While local incentives are important to protecting resources, incentives at national and global scales also are essential to the success of conservation. To assess benefits and costs, Kremen et al. (2000) compared estimates of benefits from the Masoala ICDP at local, national, and global scales. The results from their opportunity-cost scenario showed how sustainable harvest versus large-scale timber clearing would benefit local communities, the national government, and the global community. These results have strong implications for long term sustainability of not only the Masoala site, but for protected areas throughout Madagascar.

Kremen et al. (2000) found that, at the national level, the highest short-term return would come from large-scale industrial forestry concessions. The scenario is different at the local and global scales, however. Under the assumption that the forestry concessions would be foreign-owned, the local communities would benefit more from long-term sustainable harvest than from commercial timber harvest. At the global scale, the greatest benefit is also from protection of forests. Loss of the forest would cost the international community an estimated U.S. \$68 to U.S. \$645 million, based solely on the area's contribution to reducing greenhouse gases. Thus, both the local and global communities benefit from forest protection, whereas, at the national scale, the greatest economic payoff would be to sell off the forest for timber concessions. This so-called "split-incentive" situation suggests that continued pressure on national government through financial and political incentives may be critical to long-term park protection.

Work is underway to estimate the costs of managing the entire protected area network (national parks and conservation

sites). Between 1997 and 2003, U.S.\$50 million, mostly from international donors, was spent on Madagascar's protected area system. However, benefits at the national level exceeded this figure by 25%, through water delivery, erosion avoidance, and ecotourism revenue (Carret and Loyer 2003). This study changed the government view on the economic value of protected areas, and it was decided that a trust fund was needed to ensure that the planned reserve network would receive the required operational and management funds. To plan for this trust fund and determine the core costs for the forthcoming expanded network, efforts are underway to model expected costs.

The cost model being developed is innovative in that it takes into account priorities for management by considering overall biodiversity values as well as threat levels facing the reserve. Specifically, management costs allotted to a protected area depend on (1) the importance of the area for biodiversity, (2) the strategic function of each area (i.e., potential for developing research, ecotourism, or educational opportunities), (3) the size of the area, and (4) the threat level. Table A shows the number of park wardens required based on these parameters. The model incorporates supervisory, administrative, and equipment costs based on the number of wardens. This adaptive and predictive cost tool allows a cost estimate for each new site proposed to the system. It provides the global costs of managing the entire reserve system as well as cost by site over years. This tool will not only provide the trust fund and donors with a transparent analysis of anticipated costs of managing the network, but will serve as the basis for a cost accounting and monitoring system for the national governing agency. These estimates also help conservationists and the Madagascar government work together to leverage the required funds.

Protected Areas: Providing Promise for Madagascar

There are many reasons to believe that a strengthened and expanded protected area network and expanded conservation measures will make a difference in stopping extinction on Madagascar. Compared with an average annual rate of loss during the 1990s of 0.9% per year, deforestation from within protected areas was only 0.04% to 0.02%. Species also appear to be faring better in protected areas, as reef fish biomass is greater within the relatively new Masoala National Park

(about 810g/m²) than outside (525 g/m²). The annual burning of the Alaotra marshes declined from 32% to 2 % from 2000 to 2002. At the landscape scale, the Zahamena-Mantadia priority conservation corridor experienced one-third the forest loss (2.2%) than the neighboring area (6.7%). Furthermore, Madagascar has invested heavily in its National Environmental Action Plan over the last 10 years. A new Malagasy Parks Service has been established that is helping to professionalize the service and implement management plans.

From Priorities to Projects

Within the planning process for increasing Madagascar's protected area network, there are continued efforts to identify the gaps in protected areas. Once the gaps are identified and new areas for protection proposed, projects will be initiated to help conserve biodiversity values as intended. The site-conservation process requires three elements: an international donor interested in investing in biodiversity, a "conservation broker" that has contact with both the donor and local groups working in the area (usually an international NGO or similar body), and a self-motivated and self-sustaining, field-based NGO network that manages biodiversity based on a general recognition of the economic and environmental benefits that this brings. Implementation of conservation programs is increasingly done at the landscape or biodiversity scale. Rarely can site conservation be achieved by focusing solely on the site of interest; competing interests and threats are too strong for narrow conservation solutions.

The Menabe region of western Madagascar provides an example in which many conservation interest groups are coming together to realize on-the-ground conservation projects that are desperately needed. The Menabe is a genuine hotspot within a hotspot and one of the most important conservation priorities in Madagascar and Africa. The forest is one of the few sites on Earth where baobab trees grow in dense colonies. Indeed, Grandidier's baobab (*Adansonia grandidieri*), one of the largest and most beautiful, is probably functionally extinct outside this area. Menabe's rich biodiversity is under enormous human pressures that have led to a 25% loss in area over the last 40 years. This rate of loss has accelerated in the last 10 years.

Illegal slash-and-burn agriculture to cultivate maize has been the most important cause of forest loss in recent years. The soils of the region are sandy, dry, and poor, and once the organic matter in standing vegetation has been used up, crop yields diminish exponentially and the farmers are forced to move on. The second key threat is logging. While the direct impacts of tree felling seem not to have a great short-term impact on most forest biodiversity, additional hunting and increased risk of fire post-logging often means that wood-cutting ultimately leads to destruction of the forest. Therefore, long-term conservation is difficult to reconcile with logging with-

TABLE A Amount of Management Allotted to a Protected Area Based on Threat, Biodiversity Values, and Size

Protected area		
Attributes	Size in hectares	Hectares/warden
High threat with exceptional biodiversity	5000–20,000	1500
	20,000–60,000	3000
High threat with high Biodiversity	5000–10,000	4000
	More than 10,000	6000
Low threat with higher exceptional biodiversity	Independent of size	7000

out significant investment in monitoring, oversight, and enforcement, all of which have been absent up to now in the weak policy and government context.

To implement conservation goals in this region, the Regional Development Committee, helped by a range of national and international NGOs, is working to engage local communities and regional authorities in conservation, and support their capacity to manage the biodiversity resources in the region. Additionally, they work to help develop economic conditions that support conservation. Improved local capacity and a more favorable environment for sustainable economic activities will address systemic conditions that enable these threats to persist. Current conditions and expected change due to conservation projects being implemented in the region are listed in Table B.

More favorable conditions will promote access to viable livelihood options compatible with the long-term conservation of the corridor's biodiversity. This will help to address proximate threats that cause loss of high-priority habitats and will improve community, local, and national government capacity to monitor, manage, and control forest use in the following ways:

- Dramatically increasing and widening the economic benefits from biodiversity-friendly activities such as ecotourism
- Making sustainable agricultural practices more attractive and economically viable than slash-and-burn practices
- Providing long-term sources of wood for charcoal, building materials, and firewood through community management and private sector involvement
- Creating a commercially- and ecologically-viable timber production system

Meeting these objectives is only possible because of revived interest of local NGOs in collaborative processes to address biodiversity concerns in the region. Fanamby and Durrell Wildlife Conservation Trust are two NGOs that have been leading this effort. They work with the National Waters and Forests Authority, the Center for Professional Forestry Training, the German Primate Center, ANGAP (National Protected Area Management Agency), local community groups and other local

NGOs, and mayors. This work is chiefly aimed to build local capacity to design and implement forest management plans and to enforce regulations. Durrell Wildlife Conservation Trust also monitors the conditions of wildlife and runs an education and awareness campaign to decrease bushmeat hunting, wildlife trade, and illegal logging. Activities of the collaboration include (1) increasing participation in rural resource management planning, (2) identifying the highest biodiversity priority areas, (3) fostering broad support for conservation enforcement, and (4) promoting the development of private sector forest plantations to meet local demand for wood, charcoal and firewood.

A collaborative approach has much to offer. For example, in one area the local population has long been hostile to conventional development action and the area was considered a lost cause. However, recent negotiations with village elders for a traditional Malagasy law, or *dina*, has resulted in a substantial reduction of forest cutting and an openness to new income-generating activities. The key to project sustainability is developing the capacity of regional and local stakeholders to benefit from the sound management of environmental resources, especially biodiversity. While some investment in biodiversity conservation will always be required, the overall strategy is to develop the technical capacity of the region so that stakeholders in Menabe are independently capable of accessing investment in biodiversity conservation. The economic opportunities offered by endemic biodiversity, especially in the context of ecotourism, are likely to contribute substantially over the long term to the very depressed economy of the region. Current agricultural and logging processes are totally unsustainable, but opportunities exist to move these sectors away from resource mining and into genuinely sustainable practices.

One important aspect of sustainability is social sustainability—the capacity of the region to absorb the changes that are necessary for the development envisaged and to establish the skills and institutional capacity and mechanisms to sustain the changes. The current constraint is the combination of very poor management oversight and a very depressed local economy that has little or no scope or motivation for investment. With this program, the partners hope to overcome both of these con-

TABLE B Current Problems Facing the Menabe Corridor and Improvements Expected from Conservation Collaboration

Current systemic conditions	Expected change
Low local institutional (community, government, and NGO) management and technical capacity	Improved local and regional capacity for natural resource management
Inadequate protection of priority biodiversity areas within the corridor	Targeted investment in biodiversity conservation in most important areas
Government ownership of natural resources leading to land-grabs in forested areas	Transfer to local communities of management rights and economic benefits derived from sustainable natural resources
Unregulated forestry sector, with local forestry administration often heavily involved	Improved compliance with national forestry legislation
Inadequate local benefit from biodiversity conservation and low community support for conservation	Increased local knowledge and participation of the local population conservation in sustainable livelihood options resulting in support for biodiversity

straints and encourage those initiatives that are already clearly manifest in the region.

The Malagasy as Stewards

“Tsy misy ala, tsy misy rano, tsy misy vary”

The Malagasy recognize that the fate of the forest is their own. As the above saying goes, without forest, there is no water, there is no rice. Many efforts underway are channeling international interest in biodiversity conservation to the local communities who are neighbors to critical habitats. For example, half

of all entrance fees to parks now go back to the local communities. Conserving the country's unique heritage into the future will certainly pose many challenges, but the actions taken by the country's leaders are providing great hope for the future of this hotspot. While all acknowledge the importance of Madagascar for global biodiversity, there have been many who have questioned whether saving the hotspot would be worthwhile, or even feasible. Fortunately, Madagascar has recognized its own position as unique home to biodiversity, and is making optimists out of many who once doubted that anything could be done to save the country from an extinction crisis.

CASE STUDY 3.3

Key International and U.S. Laws Governing Management and Conservation of Biodiversity

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A primary focus of conservation biology is on understanding how one species—*Homo sapiens*—has affected life forms and ecosystems across the planet. If conservation biologists wish to build knowledge that is not only relevant to making choices about the future of Earth's biological resources, but is indeed influential in shaping this future, it is imperative that they develop at least a good working knowledge of social decision-making processes and regulatory systems in addition to honing their scientific expertise. Here, I summarize some of the major International and U.S. laws that influence biodiversity conservation. See Box 3.3 for a short description of other national biodiversity laws.

International Legal Regimes that Affect Biodiversity

International law is unique in that, unlike individual nations' systems of governance, there is no global sovereign with recognized authority to impose rules for conduct. This means that much of international law actually consists of agreements by countries that choose to cooperate with one another toward a specific goal; these agreements typically take the form of treaties, conventions, and voluntary participation in international organizations. The following discussion summarizes some of the agreements most important to managing and protecting biodiversity.

The Convention on International Trade in Endangered Species of Wild Fauna and Flora

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)—first opened for signature in 1973—attempts to regulate international trade in species

whose existence is or may be imperiled as a result of commerce and other trafficking. The agreement regulates only international trade in designated species and their parts; it does not attempt to govern habitat management or other species management decisions made by individual countries.

CITES' trade restrictions apply only to species (and parts or products made from a particular species) that member countries vote to add to one of the convention's three appendices. Species that appear in Appendix I—the most imperiled classification—are subject to the most stringent trade restrictions, including a ban on international trade for “primarily commercial purposes.” Facing lesser threats, Appendix II species may move in international commerce, but like those species in Appendix I, any shipment must be accompanied by an export permit. CITES does not set up any sort of international authority to implement and enforce the convention; accordingly, each individual country bears responsibility for making necessary findings and issuing required permits. The agency that serves as the “Scientific Authority” for the government of an exporting country must certify that the transaction “will not be detrimental to the survival of that species” in the wild. However, nothing in CITES or its implementing documents defines what constitutes a “detrimental” impact to Appendix I and II species. As a result, each country's Scientific Authority must formulate and apply its own meaning of this term.

Finally, any CITES member country may unilaterally add a species to Appendix III. Appendix III species are subject to restrictions only when the trade originates from the country that listed the species; this provision thus allows individual countries to regulate international commerce in a species that is in trouble only within that country.

Convention on Biological Diversity

The Convention on Biological Diversity (CBD) was opened for signature in 1992 at the Earth Summit in Rio de Janeiro, and now includes 188 countries as parties (but not the United States). The agreement is the centerpiece of the international community's efforts to craft a comprehensive approach to conserving biological diversity. Administratively, a Secretariat headquartered in Montreal serves as the permanent body for day-to-day business, and a Conference of the Parties takes place every two years.

The CBD requires countries to develop national strategies "for the conservation and sustainable use of biological diversity." In meeting this goal, parties pledge to carry out a litany of conservation actions, including creating or maintaining a system of protected areas, making efforts to restore degraded ecosystems and recover threatened species, eradicating nonnative species, pursuing programs for *ex situ* conservation, and using knowledge derived from "traditional lifestyles" of indigenous communities to foster biodiversity protection as well as sustainable use of biological resources. However, the CBD spells out these obligations only in very general terms, leaving the task of deciding precisely the sort and extent of biodiversity protections and programs to adopt to individual countries with help from advisory committees. The agreement also specifies that developed countries have a responsibility to provide "new and additional financial resources" to their less-developed counterparts; and in a telling nod to the link between economic status and ability to pursue conservation objectives, it notes that developing countries' adherence to their commitments under the convention will depend largely on the extent to which developed countries follow through with transfers of funds and technology to their less well-off neighbors.

The Convention on Biological Diversity also attempts to tackle the sensitive issues of access to and use of biological and genetic resources. It holds that each country has a right to control access to its biological resources, and that use of such resources requires prior informed consent of the nation of origin; a country's consent can be contingent on reaching "mutually agreed terms," (i.e., payment). The agreement also provides that developed states have a responsibility to share technologies and biotechnologies with countries that are not as well off; concern about how this provision affects intellectual property rights has proven to be one of the most significant obstacles to U.S. ratification of the convention.

International Habitat and Ecosystem Protections

There are a number of international efforts to identify and protect either ecosystems in general or specific types of ecosystems. The following paragraphs summarize three of the most prominent.

The United Nations' Educational, Social and Cultural Organization's (UNESCO) Man and the Biosphere Programme provides an institutional umbrella for a series of international

Biosphere Reserves. UN member states, acting on a purely voluntary basis, nominate for inclusion within the system areas within their jurisdictions that already receive protections under domestic legislation. Nominated areas must meet a list of UNESCO criteria, including a requirement that a proposed reserve "contribute to the conservation of landscapes, ecosystems, species and genetic variation," and encompass "a mosaic of ecological systems representative of major biogeographic regions." While formal designation as a Biosphere Reserve brings a measure of international recognition, there are no international standards for management of these reserves; national laws supply the sole directives for protecting biodiversity and managing human activities in these areas. More than 400 Biosphere Reserves have been designated in 94 countries.

The Convention on Wetlands, also known as the Ramsar Convention after the city in Iran where it was originally signed in 1971, sets forth a process for identifying important wetlands analogous to that of UNESCO's program for Biosphere Reserves. The 138 countries that have signed the convention pledge to designate at least one wetland within their borders for inclusion of the convention's "List of Wetlands of International Importance," as well as to include wetland protections in their national land use planning. Again, national and local laws provide the exclusive management standards for wetlands included on the list, which now includes over 1300 wetland areas covering over 100 million hectares.

Lastly, 13 marine or large freshwater areas are the focus of coordinated management and protection efforts under the United Nations Environment Program's Regional Seas initiative. Working with UNEP, neighboring countries develop an "Action Plan" for coordinated action to conserve and manage a regional sea. These plans typically set out broad "framework" strategies that rely on more specific international conventions and protocols among the countries surrounding a regional sea to initiate steps toward implementing the Action Plans' broad outlines. Such agreements also usually rely on national laws to actually carry out identified actions. While some Regional Seas programs, such as that covering the Mediterranean, have developed a number of conventions and protocols that countries have integrated into their national laws, other programs exist mainly on paper.

Federal Laws in the United States that Affect Biodiversity

The federal government in the United States has regulated various elements of biodiversity for over a century, but many of the most prominent laws date back only to the 1970s. The U.S. has a number of important statutes that deal with biodiversity, a fact which itself provides insights into this complex arena: On one hand, the many laws dealing with biological resources serve as evidence of the country's recognition of the importance of biodiversity and the United States' leadership role in crafting laws to manage and protect it; on the other hand, this multitude of not-always-consistent laws and policies illustrate

the federal government's fragmented approach to the natural world.

Endangered Species Act

Since 1973, the Endangered Species Act (ESA) has served as the United States' principal wildlife conservation law, and its high-profile controversies coupled with a public fascination with endangered species have made this statute the country's (and one of the world's) best-known biodiversity protection schemes. It provides a number of substantive protections for species classified as either endangered or threatened, including mechanisms for conserving not only individual organisms, but their habitat as well. Two federal agencies, the U.S. Fish and Wildlife Service and National Oceanic and Atmospheric Association (NOAA) Fisheries (collectively "the Services"), are responsible for day-to-day implementation of the law.

Particularly in more recent years, determining what groupings of organisms are eligible for protection under the ESA has generated substantial controversy. The law defines "species" eligible for protection to include, in addition to full species, "subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." It is important to note that in formulating its legal definition of species, U.S. Congress drew a distinction between vertebrates, plants, and all other species. Populations of vertebrates can thus be listed in some places even if they are abundant in other parts of their ranges; insects, plants, and other invertebrates must face wholesale elimination at the species or subspecies level before they can receive legal protections under the ESA. However, protracted and sometimes rancorous debate has marked efforts to determine precisely the meaning of a "distinct population segment" of vertebrate species; a policy adopted by the implementing agencies in 1996 considers two primary factors—whether a given population is (1) "discrete" from other populations of the same species, and (2) "significant" to the species as a whole.

Rather than providing biologically specific definitions of "threatened" and "endangered," to guide the Services in making listing decisions for eligible species, the ESA contains a list of factors that the agencies must consider in making listing (as well as delisting) calls. This includes a litany of biological threats such as habitat destruction, disease, and over-harvest, as well as a catchall category that encompasses any "other natural or manmade factors." Significantly, the statute also specifies that a species can receive the law's protections as a result of "the inadequacy of existing regulatory mechanisms" to ensure the species' future. After listing a species, the appropriate service must also designate its "critical habitat," which the law defines as the habitat essential for the species' recovery. Unlike when making listing decisions, an agency may consider economic and other nonbiological factors in designating critical habitat.

The ESA contains two key protections for species listed as threatened or endangered. First, actions carried out or author-

ized by federal agencies cannot result in impacts that would "jeopardize the continued existence" of listed species or "destroy or adversely modify" designated critical habitat. The Services have generally interpreted these two standards to prohibit similar levels of impact; an agency action must put in doubt the future of the entire listed species to run afoul of these restrictions. Second, the law prohibits anyone—private landowners included—from "taking," (i.e., killing or injuring) a listed species. Regulations define the term "take" broadly to include habitat impacts that result in death or injury to members of a listed species. This provision of the law has generated considerable opposition because it effectively gives the federal government wide authority over land-use decisions across the country, a power traditionally exercised by state and local governments. However, two factors have helped to keep controversies over the ban on take below the boiling point. First, Congress amended the law in 1982 to add the ESA's so-called Habitat Conservation Plan (HCP) provisions, which allow the Services to grant a permit that allows some take of listed species in exchange for an agreement on the landowner's part to adopt at least some land-use limitations for the benefit of these species. Additionally, the federal government has (unofficially) adopted a rather relaxed stance on enforcing the ESA's take prohibition.

Finally, the ESA requires the Services to formulate "recovery plans" for listed species. These plans spell out specific measures to improve the status of the species they cover, and must include "objective, measurable criteria" that, when achieved, will trigger a process to delist the species as "recovered." Agency statistics reveal that while the populations of many species listed as threatened or endangered have stabilized, few have actually recovered. The fact that there is no clear legal mechanism requiring implementation of recovery plans probably plays a role in the ESA's mixed record of conservation successes.

National Forest Management Act

Enacted by Congress in 1976 after a series of controversies over logging practices on federal land, the National Forest Management Act (NFMA) sets management standards for the 192 million acre national forest system. This vast area encompasses some of the most valuable—as well as most intact—habitat remaining in the contiguous states. These lands also harbor substantial economic and recreational resources as well, making the trade-offs involved in national forest management among the most difficult and controversial of those facing federal land managers. To a large extent, the NFMA set up the U.S. Forest Service to face endless conflict, both internally as well as with outside interests, by making "multiple use" the touchstone of forest management. The statute encompasses this "do it all" approach by setting out only very general substantive standards—essentially giving agency officials a vaguely-worded set of marching orders to please all constituencies by both producing and protecting resources.

The NFMA's provisions addressing biodiversity reflect the law's broad and imprecise mandates. Each national forest must prepare a land-management plan setting forth the overall blueprint for forest management, but the plans' specific provisions for biodiversity are largely influenced by interpretations of vague statutory requirements. The law directs the Forest Service to "provide for diversity of plant and animal communities based on the suitability and capability of the specific land area in order to meet overall multiple use objectives (set forth in an individual national forest's management plan)." The statute contains no definition of "diversity" or other key terms in this mandate, however, thus leaving open to the agency's own interpretation the outlines of the Forest Service's duties in this area.

For nearly a quarter century, regulations interpreting the statute's diversity mandate called on the Forest Service to "preserve and enhance the diversity of plant and animal communities, including endemic and desirable naturalized plant and animal species, so that it is at least as great as that which would be expected in a natural forest." The regulations specified that forest managers must "maintain viable populations of existing native and desired nonnative vertebrate species" found in each national forest. A "viable population" was defined as "one which has the estimated numbers and distribution of reproductive individuals to ensure its existence is well distributed in the planning area." The regulations further mandated that "habitat must be provided to support, at least, a minimum number of reproductive individuals and that habitat must be well distributed so that those individuals can interact with others in the planning area." To assist agency officials in carrying out these duties, the regulations also prescribed designation and monitoring of "management indicator species," species whose population trends the Forest Service believed would indicate the ecological effects of its management activities.

The Forest Service's interpretation of its duties under the ESA grew murky in 2000. Shortly before leaving office, the Clinton administration adopted sweeping changes to the NFMA regulations that established "ecological sustainability" as the management aim for biodiversity on national forests; this term was defined as "the maintenance or restoration of the composition, structure, and processes of ecosystems including the diversity of plant and animal communities and the productive capacity of ecological systems." However, the regulations retained a complimentary focus on species; managers were required to provide a "high likelihood" of maintaining viable populations of native and desired nonnative species, with a "viable" species defined as "consisting of self-sustaining and interacting populations that are well-distributed through the species' range."

Within weeks after they were adopted, however, the incoming Bush administration put the new NFMA regulations on hold and later published its own proposal to replace them. This interpretation of the law's diversity mandate also emphasized ecosystem-level management, but proposed to give For-

est Service officials significant latitude to depart from ecologically sustainable practices if necessary to meet multiple-use goals. Additionally, in the most significant change from previous interpretations of the NFMA's diversity provision, the new proposal dropped the requirement to maintain viable populations of forest species. Instead, the proposal called for management that, "to the extent feasible, should foster the maintenance or restoration of biological diversity in the plan area, at ecosystem and species levels, within the range of biological diversity characteristic of native ecosystems within the larger landscape in which the plan area is embedded." Whatever the shape of the new regulations, their changing and widely varied forms in recent years illustrate the broad and ill-defined nature of the NFMA's underlying legal mandate for managing biodiversity.

The Magnuson Act

The Magnuson Fishery Conservation and Management Act of 1976 (amended substantially in 1996) controls marine resources, particularly commercially valuable fish species, within the United States' Exclusive Economic Zone, the area within 200 nautical miles of the country's coastline. The statute's dual—and often conflicting—purposes are to promote a domestic fishing industry while establishing a federal program for "conservation and management" of the country's fishery resources. Eight regional fishery management councils, composed of both fishing industry officials and other interests, develop and implement "Fishery Management Plans" for each "stock" of commercially valuable fish; these plans set an allowable catch and other needed "conservation and management" requirements designed to result in "optimum yield" of a fishery.

The Magnuson Act has not prevented the collapse or near-collapse of many of the nation's fisheries. Consequently, the amended law sets out several requirements applicable to stocks that are "over-fished," which it defines as a rate of fishing mortality that jeopardizes a fishery's capacity to produce its maximum sustained yield on a "continuing basis." Within one year of a determination by NOAA Fisheries or one of the councils that a fishery is over-fished, or is likely to be over-fished within two years, the relevant council must revise its management plan to "rebuild" the stock, though this process may take up to a decade to accommodate the "needs of fishing communities."

Revisions to the Magnuson Act in 1996 added tentative steps toward protecting marine habitat and ecosystems. The regional councils must identify "essential fish habitat," defined as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity." NOAA Fisheries and the Department of Commerce must ensure that any of their "relevant programs" further the "conservation and enhancement" of this habitat. Additionally, the law sets up a process whereby other federal agencies whose actions "may adversely affect" essential fish habitat must consult with NOAA Fisheries, which in turn receives comments on the proposed action

from the relevant council. If these fisheries experts determine that an adverse impact to identified habitat is in fact likely, NOAA Fisheries provides the federal agency with recommendations for measures that would “conserve” the affected essential fish habitat. The federal agency must issue a written response that either details how the recommendations were implemented or explains why they were not.

Marine Mammal Protection Act

The Marine Mammal Protection Act (MMPA) takes a somewhat similar management approach as that of the Magnuson Act. The MMPA targets for conservation “stocks” of marine mammals, which the statute defines as “a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature.” NOAA Fisheries, the agency primarily responsible for implementing the act, must seek to maintain these stocks at their “optimum sustainable populations.” In addition to enforcing a general ban on intentionally killing or injuring marine mammals, the agency must take steps to reduce the incidental impacts of fishing operations on marine mammal stocks suffering levels of mortality that exceed their “potential biological removal levels.” The latter is calculated according to a detailed statutory formula that provides the number of animals that can be “removed” from the population by human-caused mortality. If this level is exceeded by incidental mortalities from commercial fishing operations, NOAA Fisheries must develop “take

reduction plans” that place mandatory conditions on these fisheries to reduce marine mammal deaths.

The MMPA obliquely encompasses ecosystem conservation in its conservation scheme. The law emphasizes that “stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element of the ecosystem of which they are a part,” and thus includes ecosystem health as a factor in determining stocks’ optimum sustainable populations. The statute also specifies that “efforts should be made to protect essential habitat” of marine mammals, but establishes no substantive standards or binding requirements to actually carry out such actions

Conclusion

Future human efforts to better manage and protect the planet’s biological riches will depend on innovations in both the sciences and the world of policies and regulation. A broad array of international and domestic regulatory regimes already play a significant role in shaping the status of biodiversity, but thoughtful input from the scientific community could make their implementation and evolution vastly more effective. Such contributions, however, can only come from conservation biologists and other scientists that have developed a sound working knowledge of these laws and policies. Better integration of science into law and policy through the work of new generations of professionals is one of the keys to sustaining biodiversity.

Summary

1. Human impacts are a pervasive facet of life on Earth. Increasing numbers of humans and increasing levels of consumption by humans create conditions that endanger the existence of many species and ecosystems: Habitat degradation and loss, habitat fragmentation, overexploitation, spread of invasive species, pollution, and global climate change.
2. Many threats are synergistic, where the total impact of two or more threats is greater than what you would expect from their independent impacts. Also, many threats intensify as they progress. Further, populations often suffer from genetic and demographic problems once they are pushed to low density or small sizes. All these factors make it more difficult to design effective conservation strategies.
3. Extinction can be either global or local, where a species is lost from all of the Earth or from only one site or region, respectively. In addition, ecological extinction can occur when a population is reduced to such a low density that although it is present, it no longer interacts with other species in the community to any significant extent. All these forms of extinction can compromise community functioning, perhaps leading to further losses.
4. Paleontological evidence reveals a long history of human-caused extinctions, although many may have resulted from an interaction between human hunting or species introductions and climate or habitat changes. Extinctions can cause cascade effects, where a first extinction indirectly causes secondary extinctions of species strongly interacting with the first. Extinction of dominant species, keystone species, or ecosystem engineers, as well as the introduction of such species, all can cause cascade effects.
5. The IUCN Red List of Threatened Species is the most comprehensive source of information on patterns of global endangerment. Overall, 41% of all evaluated species are threatened. Only a few taxa have been comprehensively surveyed (mammals, birds, amphibians, and gymnosperms), and all show high fractions of threatened species. Habitat loss and degradation is the leading cause of species endangerment.

6. Roughly one third of the species in the United States are threatened, the majority by habitat loss and degradation. Freshwater mussels are particularly threatened, as are other freshwater taxa, showing that human impacts have been particularly large on aquatic systems.
7. Attributes of species that confer rarity or specialization seem to increase vulnerability to extinction among many creatures, on land and at sea. Species with low reproductive rates are vulnerable due to the rate of extreme changes, and are particularly vulnerable to overexploitation. Island endemics and species with small population sizes are highly vulnerable to perturbations. Island endemics are particularly vulnerable to introduced species, especially when those species are from guilds not represented on the island.
8. Economic and social changes over the next century will have a large impact on the degree to which biodiversity is compromised over the next century. The extremely large number of people in abject poverty compels us to actions that will help these populations, but this need not be at the expense of biodiversity. Changes in consumptive habits among people in China and India will have enormous impacts on global biodiversity.
9. International agreements, laws and regulations are critical tools for slowing biodiversity losses. These policy instruments range from very comprehensive and powerful to more limited in their power and use. At the 2002 Johannesburg World Summit on Sustainable Development, 190 countries committed to reduce biodiversity losses significantly by 2010, which has become a rallying point for biodiversity conservation during this first decade of the 21st century.
10. Strategies to reduce biodiversity losses focus on prioritizing places to work, understanding the causes of declines, and creating strategies that will be effective

in reducing threats. Although efforts focused on ecosystems and landscapes are more likely to be effective in conserving multiple layers of biodiversity, strategic approaches often act on the site or species level.

Please refer to the website www.sinauer.com/groom for Suggested Readings, Web links, additional questions, and supplementary resources.

Questions for Discussion

1. How have anthropogenic threats to biodiversity changed over human history? Which do you expect to be the most important threats in 2050?
2. Despite considerable efforts, we know very little about the status of most of the world's species. How can we improve our knowledge on species endangerment? What kinds of information might be most helpful to garner, and why?
3. How can we use information on endangerment to motivate more conservation-oriented policies? What kinds of information are particularly persuasive to you? How might they serve to persuade national or local government officials?
4. Are any species "expendable"? Given the limited resources we have for conservation, how should we prioritize conservation efforts among species? Should we give up on those most likely to go extinct?
5. In two or three decades' time, your children or other youngsters may ask you a question along the lines of, "When the biodiversity crisis became apparent in its full scope during the 1990s, what did you do about it?" What will your answer be?