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WHAT LOSS OF ECOLOGICAL COMPLEXITY MEANS FOR THE WORLD

The dodo (*Raphus cucullatus*), known primarily for being dead, was a substantial, flightless bird that, at 23 kg, was about twice the size of the largest Thanksgiving turkeys. It was endemic to Mauritius, a set of islands east of Madagascar, and was first discovered by Europeans when Dutch sailors landed there in 1598. Typical of birds on isolated islands without mammalian predators, the dodo was "fearless" and sometimes used for food by European sailors. Habitat destruction and the introduction of egg predators including dogs, pigs, cats, rats, and crab-eating macaques (European explorers were not noted for their care in what got left behind) played the larger role, and the last living dodo was seen sometime between 1662 and 1700. One century to extinction! It then vanished, more or less, until resurrected by Lewis Carroll in 1865. Unfortunately, being resurrected as a character in a children's book does not bring an extinct species back to life.

The polar bear (*Ursus maritimus*), a top predator exquisitely adapted to its rigorous arctic environment, emerges from hibernation in the early spring at a time when the ringed seal population has pupped. Defenseless, fat-rich seal pups scattered in snow lairs across the sea ice

Facing page: Indo-Pacific lionfishes (genus *Pterois*) have been accidentally introduced to the Caribbean. It is too early to know the impact these beautiful but voracious predators will have on numerous prey species. Photo courtesy of A.J. Hooten.

make easy prey, and the bears consume large numbers of them before the sea ice begins to break up in midsummer and this easy source of food becomes inaccessible. This spring feast represents a substantial proportion of the annual caloric intake for the bears, and the fat laid down enables them to survive the winters and produce their own offspring. So it has always been, it would seem. Except that the arctic is changing, and the sea ice is breaking up earlier in the season. Progressively warmer weather has led to break-up occurring two to three weeks earlier than was the case fifty years ago, curtailing the seal-pup feasting. Warmer weather with more rain has possibly also led to increased mortality of bears during winter due to collapse of their snow dens. The condition of the bears has declined, and numbers have also fallen. On 15 May 2008 the U.S. Fish and Wildlife Service listed the polar bear as Threatened under the Endangered Species Act, despite the political difficulty this might cause if conservation activists attempt to force curbs to production of greenhouse gases to save polar bears. Polar bears are not extinct yet, but there is reason for concern. They may not be able to adapt to the ice-free Arctic Ocean that appears to be around the corner.

Dodos failed quickly, many other species have failed since, and polar bears are just the latest in a long list of species that appear to be having trouble surviving in the modern world. Dodos and polar bears, along with creatures such as pandas, humpback whales, chimpanzees, whooping cranes, tigers, albatrosses, and monarch butterflies, are among the threatened species that have attracted the most attention (and it is for this reason that they are called "iconic" or "charismatic"), but it is the smaller, far less well-known organisms threatened with extinction that should concern us more. There are somewhere between five and fifteen million species of eukaryotic organisms, including humans, polar bears, Atlantic salmon, honeybees, elkhorn corals, *Amanita* mushrooms, giant kelp, Bermuda grass, and white pine, alive on Earth at the present time. The numbers of prokaryotes—bacteria and blue-green algae—and of viruses are much less precisely known but still substantial. All of these organisms play roles in the ecosystems that sustain us. While extinctions of species have always occurred, the rate of extinctions has vastly accelerated. Although the rate averaged perhaps one species per million per year over the past sixty-five million years, it has increased to nearly one thousand species per million per year today. This means that about

0.1 percent of all extant species disappear every year, and the rate continues to increase. For the most part, we are the cause.

In reality, the extinctions are just the sharp tip of a much larger problem. Our activities are causing a substantial simplification of the earth's ecosystems—a loss of redundancy, diversity, and biomass. We touched on this problem in chapters 1 and 2 and again in chapter 6. Here we explore the changes that are happening and the possible consequences for ecosystem function and for us. I'll deal with extinction first and then turn to ecosystem function and the environmental services we depend on that may no longer get delivered as a result of biodiversity loss.

HOW WE CAUSE EXTINCTIONS

Species are going extinct for a variety of reasons. We carve up their habitats into smaller and smaller, more isolated patches, sometimes to the extent that the patches become too small to sustain populations of viable size. We pollute their habitats in a variety of ways, with chemicals or other wastes that may have much more deleterious effects on them than on us. We usurp their habitats to our own ends as farms, towns, and strip mines, often making them unsuitable for many of the native species to continue to survive there. Our tendency to subdivide, eliminate, or pollute habitats plays by far the largest role in eliminating other species; however, we also sometimes compete with them for resources other than habitat, and we often harvest them as resources ourselves. Finally, by transporting other organisms around the world we introduce exotic competitors, predators, or pathogens to their environments. Our activities are so extensive and create such big stresses for other species that we are now witnessing a rate of loss of species through extinction that is as rapid or more so than at any past time, and there are plenty of signs that the pace of loss is increasing. We are at the start of the Holocene mass extinction event, and we are the cause.

Our impact on extent and integrity of habitat can best be seen in time-series maps of forested land, whether in North America, Amazonia, or elsewhere in the world. Over time, large acreages of continuous forest cover become smaller and fragmented. The same process happens with other types of terrestrial habitat, and the barriers to movement among patches can be considerable. An aerial view of a complex highway network on the outskirts of a city is a map of small patches of grassland separated by cement barriers continually patrolled by cars and trucks. To the field mouse, cricket, or frog, these patches might as well be separate universes because crossing the road is nearly impossible. To survive in an isolated patch of habitat, a species needs to maintain a population of sufficient size, and to do this it needs to be able to obtain the resources of food, shelter, and other needs in sufficient quantity. Those resources need to be present inside the patch. The patches of grassland common inside cloverleaf loops are probably sufficiently large to support adequate populations of crickets. But for frogs, which need ponds, or field mice, which need more space than crickets, they may not be large enough. Animals that got trapped there when the highway was built may live out their lives and produce some offspring, but over time harsh winters, droughts, or attention from hawks all take their toll, and populations become smaller. If the members of those populations do not have adequate food and other resources, their ability to rebuild their numbers is reduced, the chance of recovery is reduced, and local extinction is waiting. Once the species is lost from such a patch, the likelihood of recolonization is quite low—those cars and trucks again—and over time, patch after patch loses its population of that species until the species has disappeared from the entire region. While cloverleaf loops are an unusually isolated type of patch, more natural patches of habitat—fencerows, woodlots, and unplowed patches of grassland—experience the same kind of decline and loss of species. Repeat this process of habitat fragmentation in place after place, and many species become globally rare or extinct.

The effects of habitat fragmentation on extinction have been elegantly demonstrated in a long-term experimental study of Amazon rainforest. In the late 1970s, Tom Lovejoy, then at the World Wildlife Fund and now at George Mason University, wondered how large patches of rainforest needed to be to still be able to retain a reasonable proportion of their species. This question is critical to any plan to conserve biodiversity through the creation of reserves or parks, because there is little point in protecting one or more small patches of habitat if they are too small to be able to sustain populations of many of their species. Put simply, how large do protected areas need to be to be effective in conserving their species? Discussion of this question among conservation biologists was so contentious over several years in the 1970s and 1980s that it gained the acronym SLOSS (single large or several small). Did it actually matter whether one fought to protect a single large patch of habitat or made do with protecting several small patches of equivalent total area? The "several small" approach would likely be politically and financially easier to achieve.

Such questions can be argued about for quite a while, or they can be tackled using well-designed manipulative experiments[1] and thereby answered more or less definitively. Lovejoy chose to do an experiment. It was a collaborative effort between the Smithsonian Institution and Brazil's National Institute for Amazonian Research that became known as the Biological Dynamics of Forest Fragments Project. It became the largest, longest-running ecological experiment in forest community dynamics ever. Indeed, it is still producing results. Working with the companies that were felling the forest near Manaus to harvest timber and to create grazing land, his team arranged for the clearing process to leave untouched a series of twelve square patches of forest, each 1, 10, or 100 hectares in area and separated from any nearby forest by 70 to 1,000 meters. Each plot was carefully censused for a variety of taxa before clearing took place around it and then was fenced to keep cattle out but otherwise left undisturbed. Then, over many years, the scientists carefully monitored changes in composition of species present and in the sizes of their populations. They showed conclusively that size does matter in this case, but also that the effect of patch size varies among species.

For example, to examine effects on tree community composition and dynamics, Smithsonian Tropical Research Institute scientist William F. Laurance and colleagues mapped all trees in a set of sixty-six square 1-hectare plots, thirty-nine occurring within the isolated forest frag-

1. Ecologists distinguish two types of field experiments. Manipulative experiments are much like typical lab experiments in which there are experimental and control units (separate plots or populations), and a treatment is applied to the experimental units. Natural experiments take advantage of an event (such as a fire, a tree fall, or a storm) that has occurred and compare plots or populations impacted by the event with ones that were not impacted, as if the event was an experimental treatment. Manipulative experiments are more powerful (they have randomization, replication, and appropriate controls in their favor), while natural experiments permit asking questions about types of events that the ecologist would not have the capacity to (or be permitted to) undertake. Lovejoy's experiment was manipulative—he arranged for specific portions of contiguous forest to be turned into isolated patches of specific size.

ments of various sizes and twenty-seven in nearby continuous forest. They then followed these sixty-six plots for eighteen years[2] to determine the effects of fragmentation. Their data, reported in *Ecology* in 1998, convincingly demonstrated that forest fragments experience a substantially higher rate of tree damage and mortality than do patches within continuous forest and that this greater damage is predominantly near the edge of the fragment. Edge forest, the outside band extending up to 60 meters inside the forest, is a different environment, with more wind damage to trees and a different microclimate that many forest species cannot tolerate well. As a consequence, tree mortality is almost four times higher in edges than in the fragment core (4.01 percent per year in edges, 1.27 percent in the core). This difference is a permanent one, not one that disappears a few years after fragment creation. Because of these strong edge effects, small fragments, which have a much higher proportion of edge to total area, show very different dynamics than do larger fragments or the continuous forest, and these dynamics lead to loss of many species and general reduction in average age of trees remaining. Laurance and colleagues found that fragments needed to be from 100 to 400 hectares in size[3] before they were large enough to resemble continuous forest in the dynamics their tree communities exhibited.

Similar results have been obtained in the many studies of different kinds of biota that have been analyzed. Small fragments of forest habitat do not behave like continuous forest, and a large number of small fragments, even if well protected, does not maintain biodiversity as effectively as the same area of continuous forest. While similar experiments have not been done in most other kinds of habitat, the general rule seems to be that our tendency to increase patchiness of habitat is going to have substantial effects on community dynamics and therefore on the survival of specialist species. In conservation, size really does matter, and we are naive if we believe that postage-stamp-size protected areas will suffice to preserve the biodiversity of our world.

2. I don't mean to make a big deal about this, but ecology is a science in which getting answers can take a long time because ecological systems move at their own pace. We need to understand this fact when we consider how rapidly we are changing the natural world—are we taking sufficient time to discover the consequences of our actions?

3. That's equivalent to between 187 and 747 American football fields in area, including the end zones.

To flush a toilet is to perform a task that human societies have performed repeatedly over the last four thousand years—using water to remove unwanted wastes from our immediate environment. The water, and whatever is in it, travels through pipes or channels, usually downhill, and ends up most frequently (usually after some sewage treatment) in some natural stream, river, lake, or ocean. This system works well in getting wastes away from us, and when human populations are small, it works well more generally too. The environment is sufficiently large that the wastes are diluted and pose little harm. Four thousand years ago, dilution really was the solution to pollution.

Because the system worked, there was little incentive to explore other ways of ridding our surroundings of waste products. A pity, because as we became more highly urbanized and developed more complex manufacturing processes and more chemically rich societies, we continued to send waste products of all types downhill to aquatic environments, often in considerable quantities and seldom with much thought to how well the receiving water body would be able to deal with the stuff we sent it. Aquatic ecologists have witnessed the consequences. There really is a limit to how much waste you can ship downhill to the local aquatic environment before that environment begins to choke.

This choking happens in two ways. Organic waste, the stuff the toilet was invented to dispose of, is organic matter rich in nutrients. Plants will frequently grow better when supplied with extra nutrients—whether fertilizer or manure—and there is nothing inherently wrong in placing this material into aquatic habitats. The problem is that the presence of too many nutrients leads to excess demand for oxygen by the phytoplankton and microorganisms busily breaking them down, and this excess demand depletes the supply of oxygen dissolved in the water faster than it can be replenished by diffusing through the water's surface from the atmosphere above. The result is a body of water lacking dissolved oxygen and a massive die-off of those aquatic organisms such as fish that depend on dissolved oxygen to live. How massive? At present, marine ecologists are becoming concerned at the number and size of "dead zones" appearing in the world's oceans. One of the largest and best known now forms each summer over an area about 15,000 square km from the mouth of the Mississippi westward as far as the Texas border and far offshore. Bottom waters in this zone are nearly devoid of oxygen, a condition that has major impacts on benthic fauna and important fish and shrimp resources.

The story is different for other kinds of waste, the chemicals that we wash down the drain in concentrations far greater than would normally occur in the environment and the novel chemicals that did not exist in the natural world before we invented and manufactured them. Mercury is a good example of the former; DDT, an example of the latter.

Some of our industries—notably mining and pulp and paper manufacturing—produce mercury, a highly reactive and toxic metal, as a by-product in its methylated form. Mercury poisoning is cumulative as concentrations of the metal build up in the tissues of animals and humans. Its effects are most pronounced on the nervous system, producing, in humans, Minamata disease. Symptoms of this disease include ataxia; numbness of hands and feet; general muscle weakness; damage to vision, hearing and speech; and, in extreme cases, insanity, paralysis, and death. Minamata disease was first documented in the late 1950s among residents of Minamata City, Japan, who ate fish and shellfish from Minamata Bay and the surrounding ocean. Methyl mercury released as waste from a local chemical company was incorporated into the tissues of fish and shellfish and passed to the tissues of those who ate the fish. Let's not suppose that methyl mercury affects only humans; it affects all organisms high enough up the food chain for bioaccumulation to result in significant concentrations in their tissues. (Bioaccumulation is the progressive increase in concentration of a substance within the tissues of animals progressively higher up a food web.)

DDT does not occur naturally. It's a manufactured chemical that was widely used because of its effectiveness as an insecticide. Being a strongly hydrophobic chemical, it tends to accumulate in fat deposits when ingested or absorbed through the skin. First synthesized in the late nineteenth century, it became an important insecticide during World War II and was very widely used during the 1940s and 1950s. Nonexistent in the environment before that time, it is now present in the tissues of every living vertebrate on Earth, including polar bears and humans. While DDT is relatively nontoxic to higher vertebrates, it has one important effect in birds. DDT in sufficient concentration causes birds to produce eggs with dangerously thin shells. Raptors such as hawks and eagles easily develop tissue concentrations that are sufficiently high because they feed upon mammals and other birds, and bioaccumulation means that concentrations become greater higher on the food chain. During the mid- and late twentieth century, many raptor populations crashed because eggs were too fragile to survive the period of incubation. The reduction in use of DDT since the 1970s, chiefly because its use has been banned in most developed countries, has led to the recovery of many raptor populations. DDT is also toxic to many aquatic organisms. Its widespread initial use, plus its continued legal and illegal use in many countries, particularly for mosquito control in malarial regions, has made it a widely distributed chemical in aquatic habitats, with deleterious consequences for the organisms that live there.

Mercury and DDT are just two of a growing list of chemicals we are introducing into the environment, either in concentrations rarely seen naturally or as totally new chemicals for the ecosystem to deal with. These include other heavy metals; pesticides and herbicides that can be toxic in various ways to various species; pharmaceutical breakdown products that can disrupt the endocrine systems of animals, altering sex determination and reproductive behavior and physiology; and fertilizers that overstimulate growth of plants and microorganisms. Novel chemicals are being invented every day, brought to market with limited testing for effects, and flushed into the environment with seldom much thought for the consequences. When the birth control pill was introduced, nobody imagined that estrogenic by-products from its use would find their way into aquatic environments in sufficient concentration to disrupt the reproductive physiology of fish populations.[4]

Pollution can make a habitat unsuitable for some or all of the species that usually live there, causing them to gradually disappear. By contrast, when habitat is consumed by human development, it becomes impossible for most native species to continue to live there. We consume most habitat by turning it first into plowed fields, then into towns and cities. Other habitat disappears as clear-cuts and strip mines. The extent

4. Over seven years, in a classic "whole lake" experiment, Karen Kidd and coworkers at Canada's Department of Fisheries and Oceans added the synthetic estrogen 17α-ethynylestradiol used in birth control pills to a lake in Canada's "experimental lake district" in northwestern Ontario, in concentrations that would be typical of places downstream from a small town (less than 1 to 5 nanograms per liter throughout the lake), and showed dramatic feminization of males of a common minnow—an important forage species for larger fishes in the lake.

of habitat usurpation can be gauged by a glance at the same aerial photographs that display habitat fragmentation. In Western Europe there is scarcely any natural habitat remaining. In North America there are now vast tracts of megalopolis, such as the Boston–New York–New Jersey–Washington corridor, the Los Angeles basin, or the Toronto–Hamilton crescent in Canada, that have replaced what was once near-continuous forest or open grassland. We really have taken control of vast quantities of the available real estate. By reducing the area of natural habitat, we reduce the sizes of populations of native species. Smaller populations are closer to zero, that ultimate low population size when local extinction occurs. Too many local extinctions, and another species is gone forever.[5]

While usurpation of habitat is primarily a terrestrial phenomenon (we are land dwellers), the intensity of some trawl fisheries has reached a level where the act of trawling is comparable in its impact on the benthic marine environment to plowing or clear cutting. As reported in chapter 1, in 1998 Les Watling and Elliott Norse estimated that an area of sea bottom equal to half the total area of the world's continental shelves was being trawled every year. Their estimate suggests that many parts of the world's continental shelves are being scraped clean by trawls at least every other year. The effect on the organisms that live there must be comparable to what would happen if giant combines were rolled across all native grasslands every other year to harvest a hay crop—actually worse, because the sponges and other creatures that provide structure in benthic habitats grow back much more slowly than grasses that have been cut.

We used to introduce species with scarcely a second thought. Sometimes we introduced deliberately; sometimes, accidentally. With our increasing capacity to travel quickly over long distances and ship freight all over the world, we have become progressively better at this, despite taking ever more steps to control the problem. The Polynesians purposely transported pigs, chickens, dogs, and coconut trees throughout

5. While our cities have replaced large areas of natural habitat, there is considerable benefit in encouraging urbanization rather than the suburbanization that prevails in North America. Compact urban centers house more people, use energy more efficiently, and enjoy other benefits of scale compared to the extensive suburbs and exurbs that blight many parts of this continent. European countries seem to do a better job of keeping the city from spreading into the countryside.

the Pacific; the European explorers added goats and cattle. Between the two groups, rats, fleas, mosquitoes, and cats were delivered unintentionally. Largely as a consequence, some of the highest rates of extinction of native plants, birds, mammals, and other terrestrial species have occurred on the islands of Polynesia during the last three hundred years, and Hawaii is now reported to hold more introduced than native bird species. Many island-dwelling species (remember the dodo?) are poorly adapted to terrestrial predators (rats, cats, dogs, and goats) or novel competitors. They succumb quite quickly.

We do not have to look to exotic locations in the South Pacific for examples of damage due to introduced species, however. Back in history a century or slightly more ago, the British had the quaint habit of trying to turn the rest of the world into an English country garden. Among many other examples, they brought foxes and rabbits to Australia, a whole host of "beautiful" songbirds (starlings, house sparrows) and garden plants (common dandelion, dame's rocket, purple loosestrife, rambler rose) to North America, and hedgehogs to New Zealand. Each of these "escaped" and became pest species in their new homes. Some have caused major disruptions, including loss of native species.

While we have learned to make deliberate introductions only very cautiously if at all, our accidental introductions continue. The accidental introduction of the zebra mussel, *Dreissena polymorpha,* to the waters of the Great Lakes and the Mississippi drainage has had major effects. This fingernail-sized filter feeder from the Caspian Sea came in from Europe as larvae traveling in ballast water that was then discharged in Great Lakes ports. First identified in Lake Saint Clair (the not-so-great lake between Lakes Huron and Erie) in 1988, it has become so abundant that it has eliminated numerous populations of native mussel and clam species, modified food webs by removing phytoplankton from the water column through its own voracious feeding, and caused direct economic damage through its proclivity for blocking cooling-water intake pipes in power plants and other places. Carried in the bilge water of pleasure boats or attached to neglected, mossy outboard motors on these boats, it has subsequently hopped from lake to lake across a large portion of east-central North America.

A major new introduction is currently unfolding across the reefs of the Caribbean, Bahamas, and Bermuda and along the U.S. East Coast from North Carolina south through Florida. Two species of the Indo-Pacific lionfish, *Pterois,* were first sighted off Florida in the early 1990s and are now becoming conspicuous members of the coral reef and rocky reef fish fauna from North Carolina down into the Caribbean, with populations in the Bahamas and Bermuda. Abundances are much higher in some locations than in their native habitat. These beautiful animals with long toxic fin spines are popular aquarium species and were introduced, probably more than once, when aquarium specimens escaped (in one case a hurricane led to the release of six fish) or were liberated. They are now clearly well established over a wide region. They are voracious predators of small fishes and crustaceans—their diet in the Bahamas consists predominantly of small reef fishes such as wrasses, damselfishes, gobies, and small specimens of many other families. It is too early to tell what impact they will have, but their accidental introduction is yet one more probably serious disturbance to Caribbean reefs.

We continue to harvest a number of wild species, and our harvests, as discussed in chapters 1 and 2, are frequently excessive. Our hunter-gatherer forefathers caused extinction mainly through overharvesting, but now direct harvest is far less important as a source of extinction than are all the indirect ways in which we impact other species. Still, egregious cases of overharvesting continue to exist. Currently, the sharks of the world are endangered by the quaint custom of finning, which is depleting global shark populations so that some wealthy people can have soup. Ships engaged in the shark fin trade routinely catch sharks, remove their fins, and toss the rest of the animal, often still alive, overboard. On September 25, 2009, President Johnson Toribiong of Palau announced at the United Nations that Palau had declared its entire EEZ as a shark sanctuary, where fishing of these magnificent fishes would not be permitted. As he said to a BBC reporter at the time, "The need to protect the sharks outweighs the need to enjoy a bowl of soup." Few others have been that eloquent or that clear in their understanding of this issue, and in Doha, Qatar, in March 2010, the world failed to agree that trade in several particularly endangered shark species should be halted. Palau cannot save the world's sharks by itself.

Populations of most of the world's sharks are falling because we harvest them for their fins. Rhinos are declining because we covet their horns. Bears get killed for their gall bladders, and tigers, for their whiskers and bacula.[6] Sea turtles are declining because we occupy and light the beaches they use for nesting and because we still, occasionally, harvest them for food—sometimes illegally, but usually in "traditional" hunting activities.[7] I discussed the problem of overfishing in chapter 1, and there is plenty of evidence that we tend also to overhunt, depleting populations of larger animals in an unsustainable way. We are currently overhunting African and Asian forest species for "bush meat" (see chapter 2). When it comes to certain types of fishing on coral reefs, our rates of harvest may be getting perilously close to causing numerous extinctions.

The Banggai Islands are a small archipelago of tiny islands located due south of the town of Luwuk in east-central Sulawesi, Indonesia. There is one cruise operator here who offers live-aboard dive tours. It's an out-of-the-way place. It's also home to the Banggai cardinalfish, *Pterapogon kauderni,* a small, boldly banded black-and-white coral reef fish. Its lack of a pelagic larval stage perhaps accounts for its very limited geographic distribution (only 34 square km of potential habitat around the islands). Where it occurs, it can be quite abundant, but it is susceptible to being collected for the international aquarium trade. The International Union for the Conservation of Nature (IUCN) placed the Banggai cardinalfish on its Red List as an Endangered species in 2007, when surveys had indicated that the population might have declined by 89 percent since harvest began in the mid-1990s. Its uniqueness, in combination with its diurnal habits, small size, and attractive appearance, is what makes this fish valuable to the aquarium trade. Local fishermen collect perhaps 900,000 fish per year, for which they receive US1 or 2¢ per fish. (You can buy one over the internet for $20 to $25—guess where the profit is in this fishery.) With a current total population of more than two million fish, the Benggai cardinalfish is not

6. The baculum, or os penis, occurs in some but not all mammals. Many wasteful harvests, including those for tiger bacula, bear gall bladders, and sun-dried seahorses, exist to provide humans with potions that may or may not improve libido, virility, sexual prowess, or all three.

7. For native peoples to be granted continuation of their traditional rights to hunt, fish, or harvest timber can be an appropriate way to ameliorate the effects of colonization. Problems arise when the native group uses its traditional right as a way to flaunt limits on harvest or ignore other management tools such as closed seasons. Political correctness can make it difficult to address the need for sustainability when a traditional harvest is involved.

extinct yet, but it is one of a growing number that are now being listed by IUCN because exploitation is pushing it close to extinction. The other eight species of coral reef fishes considered to be Endangered or Critically Endangered by IUCN are all larger than the Benggai cardinalfish. They include six groupers and one wrasse that are favored in the live reef fish restaurant trade, a subject explored in chapter 4.

CURRENT EXTINCTION RATES IN CONTEXT

We are responsible for most of the extinction occurring today, and the rate is somewhere around 0.1 percent of extant species per year. Species are now disappearing at a rate of about a thousand times faster than the average rate of extinction over the past five hundred million years, but there have been geologically brief periods of exceptionally high extinction rates several other times in geological history, and five of these stand out. Let's see how the present period compares to those.

We can estimate average rates of extinction during geological history by painstakingly examining the rates at which new taxa appear and old taxa disappear through the fossil record. Studies of this type indicate that the average species has a lifespan of about five to ten million years. This varies among taxa, however; the average mammal lasts for about a million years, and the average planktonic foraminiferan (a type of single-celled alga) survives some thirteen million years. A reasonable approximation, then, is that species endure from one to ten million years. The rate at which new species appear can also be estimated, in this case by examining the number of mutational changes between related species and assuming a more or less constant rate of occurrence of such changes. It takes, on average, about one million years to accumulate sufficient genetic differences for two related populations to be considered different enough to have become two species—further support for the idea of a one-million-year lifespan for species. (This is an average: species with short generation times will speciate more rapidly than those with longer generation times such as people or elephants.)

Figure 9 shows the pattern of extinction through time as revealed by the fossil record since the start of the Cambrian, five hundred forty-two million years ago. Presumably, earlier, less well-fossilized faunas experienced a similar pattern. There is an underlying low rate of extinction, punctuated with occasional geologically sudden increases in extinction

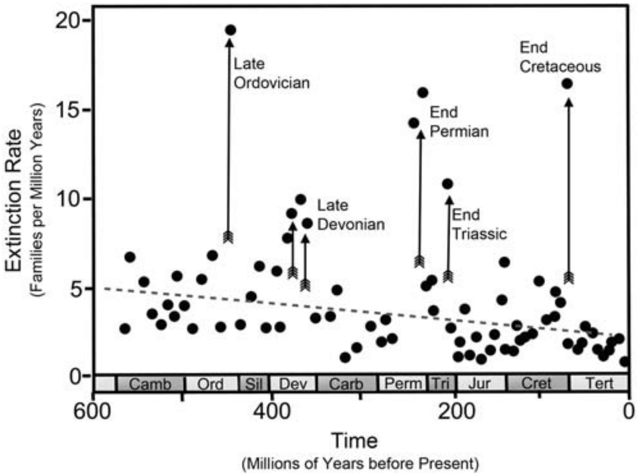

FIGURE 9. The pattern of extinction through geological time as represented by the rate of loss of families (number lost per million years) of marine vertebrates and invertebrates from the Cambrian period to the present. There are five periods, the mass extinctions, in which the rate has been noticeably higher than usual. Analysis based on records of 3,300 families of organisms. Figure redrawn from D.M. Raup and J.J. Sepkowski, "Mass Extinctions in the Marine Fossil Record," *Science* 215 (1982): 1501–3.

rate. In addition, there is a general downward trend in the average rate (number lost as percentage of existing taxa) because there has been a continuous slow increase in the total number of species present at one time as evolution has built an ever-expanding tree of branches—with more species present, the number being lost each year is a smaller percentage of the total.

The sudden peaks of extinction are termed *mass extinction events,* and we can argue about how many of these exist, depending on where we draw the line denoting "exceptionally high." Many people speak of five major events prior to the present: the Late Ordovician, Late Devonian, End Permian, End Triassic, and End Cretaceous events. (That three of the five occur at the end of geological periods is partly because so many geological boundaries have been defined based on the differences in faunal composition across the boundary.) The most extreme of the five is the End Permian event, in which some 96 percent of all marine species and 70 percent of all terrestrial vertebrates went extinct. (Other terrestrial taxa suffered as well.) The event lasted a couple of million years, with one particularly sharp peak about ten to sixty thousand years long around two hundred fifty-two million years ago. The End Ordovician event, the next most extreme, included two primary pulses of extinction a million years apart, about four hundred forty-four million years ago, and resulted in the loss of about 49 percent of marine genera. The Late Devonian extinction, most likely a series of smaller events over a period of about three to fifteen million years, occurred three hundred sixty-four million years ago and was of similar size. Fifty-seven percent of marine genera are estimated to have been lost. The End Triassic event, two hundred million years ago, was somewhat less severe: in the course of as little as ten thousand years, 20 percent of marine families and almost 30 percent of genera became extinct.[8] Finally, the End Cretaceous event, sixty-five million years ago, resulted in the loss of about 30 percent of genera and 50 percent of species over a period of a few thousand years.

How does the present rate of extinction stack up against what occurred during these past mass events? What people are now calling the Holocene mass extinction commenced during the final years of the Pleistocene with the losses of numerous large mammals. These losses of large organisms had been attributed to inability to survive a warming climate, but increasingly scientists argue that they are the result of overexploitation by human hunters. The pace of extinction quickens into historical time with the migrations of human populations into Pacific islands, Australasia, and the Americas, followed by the exploration and colonization of these same locations by Europeans. Numerous mammals and even more birds disappeared as a result, the dodo being just one. The pace has continued to quicken into modern times, and E. O. Wilson of Harvard University predicted in 2002 that we are likely to cause the extinction of two-thirds of all living species within the next one hundred years.

While 67 percent of all species is not quite as great as the End Permian's 96 percent, Wilson was not predicting that the pace of extinction would

8. Stop and think for a moment. In this least severe of the mass extinction events, in a period as short as the time since the last Pleistocene retreat, 30 percent of all genera became extinct. At present, the world's mammals belong to about two hundred genera. This rate of loss, if applied to today's mammals, would result in the total loss of sixty of these two hundred kinds of animal. Would we notice? These mass extinction events all result in massive losses in diversity.

slow at the end of those one hundred years, and one hundred years is an incredibly short time in which to lose that many species. Furthermore, Wilson's prediction is based on the effects of habitat destruction alone—the loss of species due to increase in patchiness and overall reduction of area of habitat. The effects of overexploitation and climate change and the introduction of exotic competitors, predators, and diseases will only increase the rates of loss further. Many of these newly extinct species will have the dubious distinction of having gone extinct before they were ever collected and described by science—it's difficult to be missed when you are gone if nobody knew you when you were alive. Missed or not, these newly extinct species will be participating in a mass extinction event that clearly rivals the five major ones that have gone before and is occurring much more rapidly. And we will have caused it.

Because there have been five mass extinctions in the past and the world still turns on its axis, it is legitimate to wonder if the Holocene mass extinction really matters. After all, most of the species being lost are ones that are of little direct economic value to us. And, to alter the phrase slightly, if a species goes extinct and nobody is there to see, does it really disappear? Putting this perspective more positively, as long as we ensure that the species we depend on directly remain (chiefly our domesticated species), can we just engineer a world that will continue to provide for our needs in the absence of the extravagant biodiversity that presently exists? Many people, perhaps even a majority if pressed, would consider this a perfectly reasonable proposition. Yet I guarantee we will deeply miss these newly extinct species when our world becomes simplified and ecosystems cease to function as they once did. A sizeable number of biologists would agree and would consider the proposition that the predicted loss of species does not matter to be naively optimistic. I turn now to their arguments for why the Holocene mass extinction definitely does matter. However, before doing that, it is necessary to take a short side journey and discuss the concept of environmental, or ecosystem, services.

VALUING THE ENVIRONMENTAL SERVICES PROVIDED BY INTACT ECOSYSTEMS

Ecosystems provide both goods that we use and services that make our existence on the planet more tenable. The goods are easily valued economically. They include fishery and forestry products; if we include the agroecosystems that produce our food, then the goods provided by ecosystems include everything we eat.[9] The services provided by ecosystems are much more difficult to value economically because they do not usually enter our economy as services that are bought or sold. They include a broad range of communal benefits, including regulating gases in the air, regulating climate, dampening weather variability, regulating water flow, cycling nutrients, purifying waters, and so on. They also include protection of coastlines from storms—a particularly important service given our proclivity for living close to coasts—and the provision of habitat of particular types that support tourism or recreational activities or provide essential nursery habitat for valued species that live (and are harvested) in other habitats in later life.

In 1997 Robert Costanza, then at the University of Maryland and now the University of Vermont's Gund Professor of Ecological Economics, joined with a dozen colleagues to publish an article in *Nature* that attempts to value the environmental services of all natural ecosystems on Earth. They followed a logical line of reasoning to evaluate the current economic value of seventeen environmental services for the total area of sixteen natural biomes, including forests of various kinds, open ocean, deserts, tundra, and everything in between. They came up with the amazing value of $33 trillion per year (actually, the range was between $16 and $54 trillion) for these environmental services. This was a good deal larger than the total world GNP of $18 trillion at that time.

Although broadly accepted, the Costanza estimate received some sharp criticism due to the methods used, particularly the extrapolation from marginal to total value. So, in 2002 Costanza teamed up with an even larger group of ecologists and economists led by Andrew Balmford

9. Although agricultural systems differ from natural ecosystems because humans manipulate them to such a great extent, they are nevertheless built from natural components—all domesticated food species, plant and animal, originally came from wild species, and the world's agricultural soils were all created through natural geological and ecosystem processes. Further, no matter how artificial, agroecosystems ultimately depend on natural ecosystems for their continued functioning: natural systems provide them with soil, water for irrigation, raw genetic material for breeding new varieties, natural enemies of pests, pollination, beneficial soil microorganisms, microclimate modification, and so on. Loss of biodiversity in natural ecosystems will surely affect our ability to feed ourselves, particularly as the fossil fuels upon which today's agriculture is based are depleted.

of Cambridge University to use a different approach to estimate the value of conserving the world's natural systems. Their effort was described in chapter 2 as it related to forest ecosystems. They approached the problem by seeking out examples in which it was possible to compare the economic value of an area of relatively undisturbed natural habitat with that of a similar and reasonably adjacent area that had been modified and exploited. As mentioned in Chapter 2, only five studies of the three hundred they reviewed met their criterion of a comparison of relatively undisturbed and transformed habitats: tropical forests in Malaysia and Cameroon, mangrove habitat in Thailand, wetlands in Canada, and coral reefs in the Philippines. That only five existed shows how much more needs to be done to properly value natural ecosystems.

In every case examined, the difference in the value of nonmarketed environmental services between the relatively undisturbed system and the exploited one exceeded the marketed marginal benefits of conversion, often by a wide margin. Put another way, the economic gain achieved by exploiting a previously unexploited system was less than the economic loss due to the reduced capacity of the exploited system to provide environmental services.[10] Across the four ecosystems studied, conversion resulted in mean losses in total economic value (TEV) of roughly one-half of the TEV of relatively intact systems (mean of 55 percent, with a range from 14 percent to 75 percent). While there have undoubtedly been cases in which conversion of natural ecosystems to human use—clear-cut logging, farming, cities—has been economically beneficial in the broadest sense, these results suggest that at the present time, with so much of the world's surface already converted to human use, conversion of still more is not economically prudent.

Their next step was to use the estimate of the cost of conversion to human use (55 percent of TEV) to estimate the cost of documented losses in area covered by natural ecosystems worldwide—such as the seven-million-hectare, West Virginia–sized forest being lost each year. At the current rate of loss across all natural ecosystems, the economic

10. Costanza, Balmford, and colleagues measured total economic value (TEV), the sum of the value of goods (resources) exploited and entered into our market economy, and the value of environmental services, the unmarketed benefits that the ecosystem provides. In their comparisons they contrast the TEV of an unexploited piece of habitat (no goods captured and marketed) with that of a piece of habitat that had been exploited and degraded (value of goods harvested plus services remaining following exploitation).

cost of the conversion that occurs during a single year is approximately $250 billion per year, every year into the future, because that loss continues to be felt essentially forever. Read that last sentence carefully—the losses in one year cost $250 billion that year *and every future year;* the losses the next year represent *another* $250 billion that and every subsequent year, and so on. Such compounding means that there is a very substantial cost accumulating. Perhaps because this is literally mind-boggling (see chapter 5), we mostly pay no attention to it.

Constanza and Balmford go on to discuss such interesting political details as the value of governmental subsidies to private landowners to clear their forests (Cameroon) or drain their wetlands (Canada). These subsidies, which globally amount to something between $950 and $1,950 billion per year, distort the private value of conversion (making it more profitable to the developer) and are well in excess of the total of about $6.5 billion spent per year to manage natural areas being protected for conservation. A slight shift in policy on subsidies so that owners were rewarded for creating and managing protected areas would be a very useful move.[11]

Precisely because we do not usually purchase environmental services, taking such things as the purification of water in wetlands, the protection of coastlines from storm damage by reefs and coastal mangrove forests, or the regulation of run-off and erosion by forests as uncosted entitlements, these environmental services go unvalued and frequently unnoticed. Yet in many instances they are far more important than the goods or resources we harvest from the service-providing natural systems and sell into our markets. As I write this, we are undertaking an unplanned experiment to examine the value of environmental services provided by the coast of Louisiana and Mississippi (and perhaps Alabama and western Florida). By oiling this coast with product from the Deepwater Horizon well, plus copious amounts of chemical dispersants, BP is helping to show us the true economic value of nursery habitats for fish and shrimp and beaches for tourism.[12] I suspect we

11. I know it's a radical idea—that governments might spend funds to foster actions that preserve the public good instead of spending the same funds to foster private profit at the expense of the public good.

12. The Gulf of Mexico currently produces about a third of all capture fishery product in the North American market. I see no future in which our cost for seafood is not going to rise because of the Deepwater Horizon incident.

will "discover" that the value is substantial. Unfortunately, we will discover this only because we lose that value and the economic benefits that coast was routinely bringing to fishermen and tourism operators year after year, all for free. To return to our discussion of whether mass extinctions matter, we have to keep in mind the enormous value of environmental services. These are an additional benefit, beyond the value of any resources harvested, and they are normally provided free of charge. We also have to remember that the extinctions are just the end point of gross reductions in biomass that have potentially far-reaching impacts on ecosystem function.

ECONOMIC ARGUMENTS FOR CONSERVING BIODIVERSITY

Arguments for conserving biodiversity fall into three groups: the ethical, the aesthetic, and the economic. The economic arguments are the ones easiest to evaluate because they are based on science and rational cost-benefit analyses. Ecosystems provide us with various goods and services. These have value. Loss of species or gross reductions in abundances will reduce their value, and we can measure the cost per species of such loss.

The most frightening of the economic arguments is that the loss of critical species will lead to total and perhaps sudden collapse of ecosystems—the loss of the ecosystems' ability to function in important ways, such as in the cycling of nutrients, the creation of biomass through photosynthesis, and the movement of the energy fixed by photosynthesis through the different trophic levels of food webs. Such a collapse, if widespread, would have profound economic consequences and even more fundamental consequences for our well-being. This argument hinges on the notion that ecological systems are highly evolved mechanisms that carry out their functions in efficient ways and that losing parts (the species) must lead to system failure. It's an important argument, and one I will discuss in some detail. First, however, let's examine the other economic arguments.

Other economic arguments concern either the loss of goods or services provided by particular species or the loss of adaptability or resilience of ecosystems when they become simpler because of species loss. The direct economic impact of the loss of particular species is easy to assess for many species that are already directly used. The loss of economic value often precedes actual extinction, as in the loss of value of the numerous fisheries that have crashed around the world, and for species that are harvested, we can be precise about the value they represent.

Direct economic impact is harder to assess for those species that provide services. What is the value of mangrove forests along a low-lying tropical shore, and what would happen if the handful of mangrove species that provide the structure for such forests were to go extinct? Their value lies partly in their effectiveness at ameliorating the effects of wave action on coastal communities and partly in their role as nursery habitat for a variety of coastal marine species, including valuable fish, shrimp, and crab species. Our appreciation of their protective value increased following the devastating Indonesian earthquake and tsunami that created damage and loss of life to communities across the Indian Ocean and into the South Pacific in 2002. In some instances, coasts fringed with mangrove forests were far less impacted than were those lacking such buffers; many coastal villages protected by mangroves were spared.[13]

What about the coast redwood of Northern California and Oregon? It has measurable value for the timber it provides, and it has equally valid but less easily quantified value for the tourism it promotes, the carbon it sequesters, and the local weather and cycling of water it creates. Finally, there are all those species that may be able to provide goods but have yet to be discovered and exploited, and those that provide services of which we simply are unaware. Chief among the providers of not-yet-discovered goods are species that may produce novel compounds in their tissues that will turn out to have pharmaceutical or other industrial value once we discover them. The pharmaceutical industry employs many biologists to comb oceans and tropical forests for species that may yield products with therapeutic properties or that can be manipulated chemically to create valuable compounds for medicine or manufacture. Nanotechnology will undoubtedly find biological products of use as building blocks, and research using proteins or DNA molecules to build novel nano-scale machines is already well under way. While we may not know the potential economic value of a particular species at risk of extinction, a precautionary approach would

13. This story is a little more complicated: it turns out that mangroves definitely protect from modest storms and wave action but not so much from extreme storms and waves.

suggest we should not be too sanguine about rampant biodiversity loss, because some of the species lost could have had substantial value to us if they had been saved.

The loss of resilience, and therefore of adaptability, of ecosystems due to the loss of species is even more difficult to evaluate. It's a given that ecosystems generally contain numerous examples of similar species that do similar things in similar ways. The many different trees in a forest are an example. In the beech-oak-maple forests of eastern North America, the various species of tree all contribute to the canopy, and all carry out photosynthesis to build organic matter that sustains the animals and other organisms that live in the forest. It is a reasonable assumption that, over ecological time-scales, each of these species of tree has its own particular "expertise." It does best under slightly warmer, drier, colder, or wetter conditions than do other species of tree in the forest. Under one set of prevailing climatic, geological, or soil conditions, or even under one set of prevailing abundances of herbivorous insects and tree pathogens, certain of these species will be functioning at their best while others will be performing suboptimally. Overall, the forest does what forests do: converting sunshine and nutrients into organic matter and sustaining the rich array of animals and other organisms that live there. If there is a change in conditions, certain other of the tree species will begin functioning at their best, while the prior best performers will begin to perform suboptimally. The diversity of tree species present allows the forest to continue to provide its goods and services even though conditions are changing. Of course, over longer geological time-scales, any of these tree species may undergo evolutionary changes that will change its "expertise." Therefore, if climates are becoming colder and wetter over decades or centuries, many of the trees may shift their capabilities so that they become better adapted to the new conditions.

Because the forest contains a number of different canopy tree species with their different specializations, the forest ecosystem is buffered from the effects of changes in its environment. By contrast, a forest containing a single species of canopy tree will be more directly impacted by cooling trends or by insect or disease outbreaks. In this sense, the more diverse forest has greater inertia, or resilience.

The Holocene mass extinction will rob forests and other ecosystems of their diversity and will reduce their capacity to function in a consistent way despite changing environmental conditions. Many people frame this argument in the context of genetic diversity. When mass extinction removes species, it removes unique genetic patterns. These genetic patterns may be valuable for ecosystem function right now, or they may be ones that will come into their own at some future time when environmental conditions particularly favor them or when further evolution changes them into particularly well-adapted forms.

Now, how realistic are these two arguments? On one level they are compelling. The ecological world does provide us with goods and services, and loss of species does remove the goods and services they formerly provided. Further, there are undoubtedly instances of novel products yet to be discovered, and if the species capable of supplying that product is lost before the product is discovered, there has been a loss of future value. From another perspective, however, these arguments can be overstated. The very redundancy of natural systems—the several canopy tree species, the far more numerous beetle species, and so on—ensures that in many cases one or more species can be lost without any measurable loss of economic value for us. Northern forests with ten or fewer species of canopy tree function quite well, and I am far from convinced that losing a few species of tree or beetle or anything else will result in a measurable degradation of the goods and services forests provide. Only where a species provides economic benefits that cannot be provided by other species does its extinction result in demonstrable economic loss.

I am aware that my career working with diverse tropical systems may have biased me against the idea that the loss of a single species could have significant effects on an ecosystem's capacity to provide its services. When the forest has ten tree species, each species plays a more important role than if the forest has one hundred species. Still, let's agree that species losses will become cumulatively significant sooner in the less-diverse ecosystems than in the richer ones. In fact, my possible bias may be moot, given that we should be focusing not on the loss of one or two species but on the near-term loss of substantial numbers of species. When we talk of losing two-thirds of all species, we are entering a very different arena. We will not be able to lose two-thirds of all species without losing all members of particular functional groups. It is the sheer scale of the mass extinction now taking place that should be causing us to worry. The genetic diversity lost when a single species goes extinct is rarely worth worrying about. Nor in most cases are the goods and services that that single species provided. But the removal of over half the species presently on Earth is loss at a vastly different scale. It will have substantial consequences, some due to the loss of goods and services, others to the loss of genetic resiliency that their extinction will result in. The problem is not in the details of how the loss of each species will affect us economically, but in the fact that such a large proportion of species is being lost. Death by a thousand cuts is still death, even when the individual cuts are small.

The concept of ecosystem collapse as a consequence of extinction is somewhat different from the other economic arguments. This argument does not hinge upon the intrinsic value of the particular species that are going extinct but on the idea that there are ecosystem-level properties that are important for providing goods and services and that these properties will be so irrevocably changed by species loss that the goods and services will not be provided. I wrote in chapter 6 that ecosystems are less finely coevolved than the prevailing wisdom suggests and that community structure is not nearly as strongly regulated as many might claim. This perspective might support the argument that biodiversity does not matter—if community structure is relatively loose, the loss of a single species will not be expected to ripple across the community. And it could follow that the loss of two-thirds of species could still result in a biosphere that functioned much as the current one does and provided for our needs. I do not believe this chain of reasoning is correct, however. I have not changed my mind concerning community organization, but when we talk about eliminating the majority of all species, we have to recognize that ecological systems are going to be profoundly changed, sometimes in unexpected ways. We have growing evidence that ecological change can be abrupt rather than gradual, that thresholds and tipping points really do exist. It is possible the that loss of certain species will increase the likelihood of loss of certain other species strongly dependent upon them, so that the rate of loss spirals up to much higher rates than at present. It is also possible that the growing stresses on the environment caused by our activities will accelerate species loss. In both these cases, thresholds and tipping points are likely to loom up unexpectedly. So, while we know that species are going extinct at a fast rate, what we do not know at present is how far down this path of lost species we can go before the situation becomes critical and we find ourselves at the threshold of a nightmare. I would prefer not to find out.

At the present time honeybees (*Apis mellifera*) are in decline. They are suffering a broad range of problems, each of which lowers their capacity to survive and reproduce. These include the effects of pesticide use in agriculture, the introduction of disease agents due to the increased international transport of bees to supply the needs of the agricultural sector, and the reduction of habitat as farms become ever-neater checkerboards of adjacent fields. Honeybees themselves are not in danger of extinction yet because there is a substantial industry that cultivates them and distributes them to provide pollinator services to farmers. However, wild populations of this bee have declined significantly—by about 90 percent in the last fifty years in most parts of the United States—and the factors that are responsible also impact other species of bee and other insects.[14]

Insecticide use remains heavy in many agricultural crops, and the chemicals used rarely target only specific pests. In the developed world, insecticide use is also rampant in suburbia, where we have been taught to value green monocultures of grasses in preference to the whimsical diversity of meadows with their wildflowers, clover, and dandelions. And in many places there continue to be spraying programs for mosquito control. The consequences are that many insect pollinators are in decline. Loss of habitat also makes life difficult for insect pollinators and for other species such as bats and birds that play important roles as pollinators as well.

A quick survey of pollination tells us that a large fraction of plant species are dependent on animal pollinators to fertilize their seeds. Of one hundred fifteen crop species in a recent worldwide study, eighty-seven relied partly or entirely on animals for pollination, and it's estimated that about one-third of human nutrition depends on insect pollination. Further, all pollinators are not the same. Some can service some plants and not others. Different lengths of tongue, different body shapes, and

14. A somewhat analogous situation exists for the Atlantic salmon, *Salmo salar,* which is native to the rivers and streams of northeastern North America. This animal has been extirpated in many of its native rivers, due primarily to habitat alteration, but it is among the most abundant aquaculture species on the planet and is cultivated along the coasts of all continents. Probably more numerous than at any time in the past, it is not going to disappear any time soon, but *ecologically* it is approaching extinction.

different behavior when visiting a flower all play a role in determining whether a particular insect is able to extract the nectar it seeks from a particular flower (and thus whether it will bother to visit the flower) and whether it is effective in carrying pollen when it does visit a flower.

While many pollinators, such as the honeybee, are generalists, some are specialists, closely adapted morphologically and behaviorally to the structure of the flowers they service. Indeed, the close matching of pollinators and flowers in such groups as the orchids was one of the first examples of coevolution—the closely complementary evolution of a pair of species to make them particularly well adapted to each other—that attracted scientific attention. So, turning aside from the particular problems of the honeybee or even of the farmer with a field crop that absolutely needs its pollinators, what happens when various species of pollinator start to disappear? A certain amount of pollination just won't get done, and plants will fail to produce seed in the quantities they might otherwise be capable of producing. Rachel Carson's silent spring becomes a silent and unproductive spring. In time, plant species begin to disappear as well.

What about other forms of tight coevolution that would result in cascades of loss? This is where things get difficult because there simply has not been sufficient study of the extent to which species are truly dependent on one another for their continued existence in a community. The concept of the guild, or the functional group, is useful here, because in most species-rich communities it is a relatively simple task to recognize that there are particular types of species that play particular roles and that several species of each type may be present. The forest is made up of canopy and understory species of tree as well as a host of different kinds of other plants. Its animals can similarly be grouped into sets of species that do similar things, or play particular roles in the community. Loss of one or two members of a functional group can therefore be managed by other species stepping forward to carry the extra load. As with pollination, where most plants can be pollinated by more than one insect and most insects will visit more than one plant species, other coevolved relationships tend to include groups of species.

In the coral reefs of the vast Indo-Pacific, stretching west from Hawaii and Easter Island all the way to the Indian Ocean and the Red Sea, there are some behaviorally fascinating examples of commensalism, a particular form of coevolution. One of the best known is of the anemone and its anemonefish—"Nemo," to that cohort who had their childhood in the late 1990s. All but one of the twenty-eight anemonefishes belong to the single genus *Amphiprion.* They all use anemones as an obligate habitat and occur as small, permanent groups, usually with a single dominant female, resident in a single anemone. They use a variety of anemone species as hosts, preferring ones of relatively large size, providing lots of cozy space among the tentacles in which to revel. And here is the catch. All twenty-eight species never occur together, because they have different geographic distributions across that vast expanse of ocean, but many places include five, six, or more of the twenty-eight among their native species. Careful field studies have shown that the several anemonefishes present at any particular location will each exhibit definite preferences for particular species of anemone. However, every species of anemonefish can be found using more than one species of anemone, and every anemone offers space to more than one species of fish.

This commensalism is obviously coevolved. The tentacles of these anemones are toxic to most small fish, and the anemonefish either does not trigger the release of or is immune to the toxins. Both partners benefit, because the fish, gaining shelter and protection from the anemone, sometimes happens to lure other species within the anemone's reach or, more frequently, drops small food items that then become food for the host. Yet the commensalism has not developed as a strict one-to-one partnership but as a partnership between the members of two functional groups. In such cases, if one or two species of anemonefish or one or two species of anemone were to become extinct, the world would go on, and there would still be fascinating partnerships between fish and anemones.

Exactly the same story can be told of the somewhat less well-known partnership between certain burrowing gobies and shrimp that also live on reefs in the Indo-Pacific. Gobies of the genus *Cryptocentrus* grow 10 to 15 cm in length, a bit larger than Nemo, and live in burrows dug in the sandy floors of reef lagoons. Unlike many other gobies, they are unable to dig their own burrows. Instead, they team up with shrimps of several genera within the family Alpheidae. These shrimps are able excavators that build complex burrows big enough for two, or three if one is a fish. This is a true commensalism, in which both partners benefit: the fish obtains use of the burrow in return for sitting at the entrance and signaling approach of danger to the shrimp. (They usually signal by touch, and it's common to see the fish at the burrow mouth with one antenna of the shrimp draped across its tail.) While there are definite preferences for partner species, in most reef regions several species of fish occur with several species of shrimp. Once again, if one species of shrimp became extinct, the gobies would make do with whomever was left, and vice-versa.

If one searches carefully for other examples of commensal relationships, both the ones in which the partners are relatively independent, free-living organisms and the ones in which one partner is extensively modified to live within the other and does not spend time in the great outdoors, it seems that functional groups of commensals are more common than single pairs of species living closely with each other. At least this is the case in the tropics, where diversity is high (so again, my possible bias may be misleading me). In such cases, loss of one species will not lead irrevocably to loss of the partner.[15]

To summarize, studies of commensalism, in which we would expect to find very tightly coevolved species, usually reveal patterns in which several species of one type occur together with one or other of several species of the other type. The redundancy characteristic of most ecological systems, in which species commonly exist as members of identifiable functional groups, extends even to commensal pairs. This redundancy makes it relatively unlikely that the loss of one particular species will be followed by ecosystem collapse.

Therefore all three economic arguments—ecosystem collapse, loss of direct economic value, loss of environmental services—suffer the same problem. The impact of the *loss of a few* species tends to be overstated to argue in favor of working to prevent the *loss of large numbers* of species. Overstatement weakens the arguments, yet they are valid when we consider the loss of two-thirds of all species. It is quite unlikely that such heavy losses will be balanced across functional groups so that representatives of each group will remain behind. Loss of all the canopy tree species really does eliminate the forest. I would not call this eco-

15. In his 2006 book *Nonequilibrium Ecology,* Klaus Rohde provides numerous examples from the world of parasites that demonstrate the species-rich guilds of parasites adapted to life in specific regions of an organism's body and sometimes several species' bodies. Even here, the one-to-one partnership is apparently far from universal.

system collapse, but I would call it a distressingly simplified world, and one that will be economically challenging for us. Striving to prevent or at least slow the progress of the Holocene mass extinction seems, from the perspective of economic self-interest, to be a valuable goal, even if the precise arguments supporting this goal may be a good deal weaker than many believe.

ETHICAL AND AESTHETIC REASONS FOR CONSERVING BIODIVERSITY

Ethical arguments for biodiversity conservation are often reduced to "we do not have the right to cause extinctions," and aesthetic arguments to "every species is a unique product of evolution and therefore of intrinsic value that we should honor." I think these simple assertions trivialize these arguments, and while I am uncomfortable venturing outside my rational and materialistic comfort-zone, we need to explore them.

I personally believe there are strong ethical arguments for developing a more responsible stewardship of the earth. However, I was influenced, a couple of years ago, by a colleague I greatly respect who claimed that ethical arguments were not particularly helpful, because for some people they weakened the general case. He offered a counterargument: No other organism behaves ethically toward other species, and it is a gross distortion of our animal nature to argue that we have a responsibility that no other organism has—a responsibility to act in ways that permit the continued existence of all other species. By making ethical arguments for more responsible management of the earth's ecosystems, one runs the risk of having the argument "thrown out of court" because the starting premise (that ethics are appropriate) is judged to be false. Far better, he argued, to restrict the arguments to ones based on economics than to introduce a possible distraction in the form of ethics.

I think there is much merit in this perspective, because ethical arguments will not fare very well against arguments from big business concerning loss of jobs, loss of GDP, and losses in the stock market. Far too often, the environmental movement has failed to win the critical battles because economic forces have opposed what the environmental movement sought to achieve, and the environmental arguments have been a mixture of "the sky is falling" and "it's the right thing to do." In fact, as I have tried to demonstrate throughout this book, there are good, economically sound arguments for responsible environmental management. Sustainable management, in the long run, produces greater quality of life for humans than does a less-responsible approach.

Still, it would be wrong not to admit that there are valid ethical arguments that can bolster the arguments based on economics. In my view, a valid ethical argument can be based on the observation that humans appear likely to be the only living organism on the planet with the capacity to identify and understand complex causal relationships and to anticipate the future consequences of present-day actions. Given that we have these special capacities, we are obligated to behave responsibly and to avoid behaviors that are likely to result in deleterious consequences for the biosphere of which we are but one part. Deleterious consequences are such things as a substantial alteration in the rates at which species become extinct compared to rates in previous times. To behave ethically, we should, as individuals and as a species, attempt to tread lightly on this planet. In the present context, that means we should attempt to avoid actions that lead to the extinction of any species. (I think it's notable here to remember that the extinctions we have caused have rarely been deliberate; they have been the accidental but inevitable consequence of our carelessness or greed.)[16]

In essence, I am arguing that all extant species have a right to life and that we do not have the right to knowingly cause extinctions. As my colleague would say, this is a pretty wishy-washy argument, and not one based on sound scientific principles. Still, it's an argument that some people will embrace, and it has its own validity: as creatures possessed of free will and the ability to anticipate the effects of our actions, we have a special obligation, perhaps only to ourselves, to avoid behaving in a way that knowingly causes the extinction of other species. We are more civilized if we live up to this obligation.

This ethical argument requires that we accept that there exist absolutely just states and transitions in this universe against which our actions can be measured. (The argument may also benefit from a Gaia worldview, but as one who long ago rejected Gaia, I do not think it

16. The smallpox virus is a rare exception that we deliberately sought to eliminate. It would now be extinct were it not for the archived samples retained in certain government labs.

essential.) The argument does not require that we not kill other animals (although many may try to stretch it in that direction), but it does require that we avoid unnecessary or excessive killing either directly or indirectly via pollution, habitat destruction, and so on. It does not require a belief in any higher power or an expectation of punishment for behaving unethically (although it does have a place in many religiously grounded worldviews). It does require acceptance of the idea that, unlike other organisms, we somehow have had bestowed upon us (or have taken to ourselves) greater responsibility for caring for the biosphere than they have. In this regard it clearly lies outside science, and while some will embrace it enthusiastically, others will reject it out of hand because of that fact, arguing that it is neither right nor wrong to undertake actions that lead to massive extinction, cause total collapse of ecosystems, or even endanger our own future survival and prosperity. Ethics is simply not a part of the natural world, and we should be no more concerned that our actions are responsible for the Holocene mass extinction than that great asteroid was when it was about to plunge into the Yucatán Peninsula sixty-five million years ago and cause the End Cretaceous mass extinction. Some may embrace this counterargument, but I like to think I am a more sensitive (that is, sentient) individual than some large lump of rock hurtling through space.[17]

The aesthetic argument is somewhat different. It is based on the notion that every species is a unique product of evolution that will never exist again if it goes extinct. Uniqueness has intrinsic value. We should no more countenance the extinction of a species than we should the destruction of the Mona Lisa or the paintings in the caves at Lascaux. As a unique creation of the evolutionary process—the fundamental engine of existence—each species has a precious beauty that deserves to continue to exist in the world, regardless of whether it provides us with goods and services or whether we have an ethical responsibility to preserve it. As with the ethical argument, to accept this argument requires acceptance of the existence of fundamental truths, such as that uniqueness is of value. Again, this is not a scientific argu-

17. Although there is excellent evidence for the asteroid that landed on the Yucatán and reasonable deduction concerning the nuclear winter that followed, it is doubtful that this event alone caused the End Cretaceous mass extinction, which killed off species throughout the world and in the depths of the oceans. It was the cymbal clash that marked the end of a complex series of events that coalesced to create this mass extinction.

ment, and it is easy to squelch. The Taliban, who destroyed the giant statues of Buddha at Bamyan, Afghanistan, would presumably squelch it with ease.

THE UNFOLDING OF THE HOLOCENE MASS EXTINCTION

We are well into what may become one of the largest mass extinction events the world has seen. This Holocene mass extinction is occurring because of human abundances and human activities. It commenced for terrestrial species by the end of the Pleistocene and now includes marine organisms. In excess of two-thirds of all extant species could be lost by 2100, and there is no reason for the process to stop at that point. What will the world of 2100 be like?

Most larger species (coyote size and up), other than those directly cultivated by humans, are likely to be extinct or to exist only as threatened populations, with perhaps a few representatives in zoos. Truly wild landscapes (other than deserts) are likely to be nonexistent, except in parts of North and South America. Ecosystems, other than agricultural or urban ones, will be depauperate and remarkably uniform from place to place, but they will probably still function to cycle nutrients and capture energy. Environmental goods and services will be much reduced simply because of the loss of diversity of organisms. With the increased homogeneity and overall reduced diversity, there will be a much greater risk of pandemics that severely impact particular species and create massive change in ecosystem composition as a result. The risk of a species extinction that has major ramifications through the ecosystem will become ever greater as diversity falls, and our own population will be precariously dependent on just a few species to sustain its vast size.

This is not a world that I want to see, or one I want to help create. Yet I suspect it could be a sustainable world for a time, as long as we engaged in a fair amount of environmental engineering to help it along until it neared the point of final collapse. Ultimately, if our numbers and our demand for environmental goods and services remain high, it will have to collapse. I suspect the collapse will be sudden and unpleasant. At the same time, because it will be sustainable for a while yet, there is the real risk that only a few more people will be particularly concerned than are concerned at present. Increasingly urbanized populations, with increasingly virtual entertainment experiences, will watch the dying of the final wild species with no more concern than our ancestors gave to the loss of the passenger pigeon or (nearly) the bison. The dodo looks grand on a stamp or in a children's book, and there are lots of things that begin with the letter Z other than *zebra*.

To summarize, the problem with mass extinction is that there is little evidence for severe environmental consequences of increased extinction—the kind of consequences that would cause us direct harm—until the process has proceeded fairly far down the path. Ecosystems will continue to function, even as they become simplified, until suddenly they do not. The precautionary arguments for working to stem this massive loss of species are fairly weak, and when pitted against the need to make money and buy bigger cars and houses, they are unlikely to prevail. The ethical and aesthetic arguments are also weak in cultures that are strongly materialistic and selfish. As a consequence, it is going to be difficult to achieve the dramatic shift in attitudes that will be needed to reverse the trend. Yet, if we are going to solve our environmental dilemma, we have got to begin to change how we interact with the natural world. Finding the right enticements to encourage us to start down a more appropriate path is the challenge we must tackle in the remainder of this book.

While lapsing into abject pessimism is easy, there are two faint glimmers of hope. First, human attitudes can switch suddenly when the right symbol appears, and the conservation NGOs know this. Maybe we will lose the polar bear but, in that process, wake up to what we are doing to our world. Secondly, the Holocene mass extinction is not a phenomenon happening in isolation. Our activities are having many different impacts on this world. Loss of biodiversity is just one aspect of what we are doing. It is possible that some of the other consequences—such as loss of much of the Greenland ice sheet or permanent drought in many of our most important food-producing areas—will be more dramatic and will lead us to review our actions carefully. Mitigation of the effects of the large, growing, overconsuming human population will have benefits for biodiversity conservation even if the desirability of retaining diversity was not the reason for mitigation.

If we do nothing, and the loss of species continues, there remains one other important idea to keep in mind. The world has survived massive loss of species before. On each occasion, diversity has recovered, and the world's biota has become even richer in species after some time has passed. It's possible to be optimistic concerning the eventual resolution of the Holocene mass extinction. But we must also be aware that during every previous mass extinction, the species that were most dominant before the collapse were among the species that were lost. It takes considerable hubris to expect that millennia after the Holocene mass extinction has run its course, humans will still be present to enjoy the recovery of diversity. Hominids have never been a richly diverse group, and we are one thin thread out of Africa. Should we really expect to be here indefinitely? Do we deserve to survive if we take no steps to preserve the ecosystems upon which we still depend?