Ecological principles for natural habitats management

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ABSTRACT— This paper reviews the basic principles that anyone working on projects that affect natural habitats must take into consideration — kind of “everything you need to know about ecology but were afraid to ask”. It is also a quick guide to people concerned about the environment, covering the mechanisms we have to worry about which human activity may be disrupting, the extent of such damage and the extent of our knowledge, and briefly considers some of the small changes we can make in how we deal with natural ecosystems. The main threats to biodiversity are habitat loss (human encroachment), over exploitation (overkill, poaching), exotic species, ripple effects which follow the loss of species from natural communities, and environmental change (which have caused massive extinctions prehistorically, and may do so again soon). The nature of the uncertainties about how ecological systems work, the pervasiveness of species interactions and ripple effects, the complexity of natural ecosystems, and the state of our knowledge and ability to predict environmental consequences of our actions, argues for extreme caution in how we deal with the natural world. It may even necessitate a deep philosophical change in the way we think of the world and our own place in it — and especially our relationship to the other species with which we share this planet.

Introduction

Management for what? Management for timber production is a completely different endeavor from management for biodiversity, management of a coastal fishery or management to minimize the extinction risk of a particular endangered species. Yet they may sometimes have overlapping interests and often face similar sets of considerations. Only a very small part of natural habitat areas are under any form of protection. And the vast majority of nature reserves are very small indeed (<500 km^2). To have any chance of safeguarding the diversity of species we must manage both protected and unprotected areas with that goal in mind. We must manage very carefully both protected and unprotected lands, and we must obtain some level of protection for more and larger areas and more species. If a reserve is large enough, management may entail only leaving it alone or making sure it is left alone by others (protecting it from poachers, squatters, and pastoralists). At the moment, it is not clear whether any reserve is that big. And with the global scale of human activity and our impact on the global climate, all reserves will have to have some form of specific management and monitoring.

It is often said that extinction is a natural process, a part of evolution, so why should we be concerned about the disappearance of species due to human activities? New species will surely arise. A recent estimate of the present extinction rate suggests that 90 species disappear from the face of the Earth every day. The "natural", or background, extinction and speciation rates are on the order of one species per year, or a little longer. The background extinction rate for birds and mammals has been estimated at one extinction every 100 to 1000 years, based on a mean life span per species of 1 to 10 million years. Under an equilibrium assumption, the background speciation rate is comparable in magnitude. The species loss today rivals the mass extinctions at the end of the Paleozoic and Mesozoic eras, probably at a much greater rate. In the earlier mass extinctions most of the plant species survived. Now, for the first time, plant diversity is being lost at a rapid rate (Wilson 1985).

No precise estimate of present species loss can be made, because a) the number of species is not known even to the nearest order of magnitude, and b) the ranges of even the known species have not been worked out in most cases. About 1.7 million species have been described to date, nearly 60 percent of them insects. Beetles make up one half of the known insect species. Yet, 50% of the known beetle species in the world are known from only one specimen from a single locality. The Steven's Island wren is known from only one specimen and the species is thought to have been simultaneously discovered and extinguished by the lighthouse keeper's cat.

Tropical rainforest cover 6% of surface of the terrestrial surface area, yet contain at least 50% of all species (Myers 1989). Most likely the proportion of the world's biodiversity that is found in these forests is much higher (e.g. Erwin 1987). Tropical rainforests are being depleted rapidly. The estimates of deforestation rates vary due to the difficulties of classifying forests and classifying the disturbances. Some distinguish between open and closed forests, others between forest clearing and forest degradation, and so on. Rates of species loss are much more uncertain than deforestation rates. A four year search for the 266 species of freshwater fish described from the Malay peninsula found less than half (only 122) of them (Diamond 1989). No one knows how many species are being lost even before they have been described by science. May et al. (1995) review current global extinction rates, prehistoric back-ground extinction rates, and the problems of estimating them.

> *"To dismiss the current extinction wave on the grounds that extinction are normal events is like ignoring a genocidal massacre on the grounds that every human is bound to die at some time anyway"*
>
> — Diamond (1989)

Deforestation and forest fragmentation in Sao Paulo, Brazil

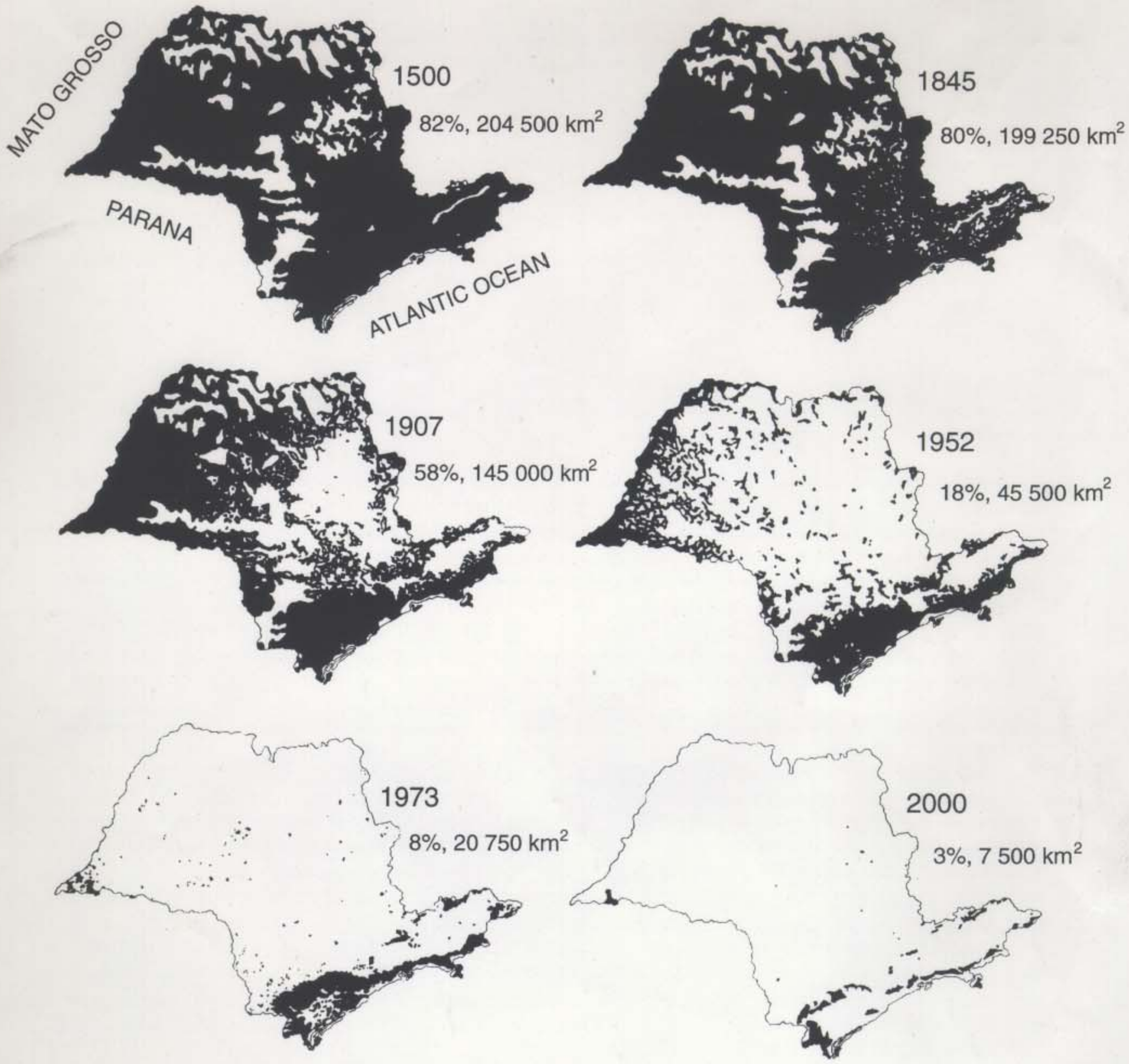

Figure 1. Depletion of forest area in Sao Paulo state, Brazil (after Oedokoven 1980). Estimated forest cover in 1500 was 81.8% of the state. The projection for the year 2000 is only 3% forest cover. Early deforestation involves clearing openings in the previously continuous forest cover. Progressive deforestation causes fragmentation of the remaining habitat, creating more and more forest patches that get increasingly isolated. Eventually the number of forest patches declines as individual patches get so small they vanish entirely.

The main threats to biodiversity are:
• habitat loss (encroachment), the biggest present and future threat;
• over exploitation (overkill, poaching), which has caused most extinctions so far;
• exotic species (Box 1)
• ripple effects, which follow the loss of species from natural communities;
• environmental change, which have caused massive extinctions prehistorically, and may do so again soon.

Habitat loss is the most important contributing factor, and it will become increasingly important in the future as habitat loss and fragmentation reaches critical levels for even more species.

Ecology sets the limit for sustainable harvesting in forestry, fisheries, agroecosystems and consequently for human population size and consumption. Consequently, ecology, in conjunction with the first and second laws of thermodynamics, sets the limits that determine whether development is sustainable or not.

Box 1. Exotic species

The science of ecology cannot predict exactly what will happen in any particular introduction, but experience with historic and prehistoric introductions gives some indication of the wide-reaching and often surprising outcomes of such events. A biodiversity crisis presently playing out its course is the inadvertently human-assisted island hopping by the brown tree snake which poses a devastating threat to bird faunas in the Pacific. Of an estimated 35 land birds once present in the Marianas, 15 fell to the islands' first human colonists, 5 more since then. 12 have survived human occupation — at least until now. The brown tree snake was introduced to Guam where it has caused the extinction of a dozen bird species, who have little defence against snakes that raid their nests. Guam now has only one species that may be considered safe, two are endangered, and one (the Marianas crow) survives but rarely breeds (Pimm et al. 1995). The snake also causes the extinction of native lizards. The snake has spread to Saipan, three islands to the north. It has also been recorded on neighboring Rota and Tinian. Oahu and Kauai have additional records and one snake was found in Texas crawling out of a shipping container that had been sealed for 7 months.

The introduction of goats to Saint Helena resulted in the total extermination of all 33 **endemic** plant species (Yablokov and Ostroumov 1991). Introduced species on the Hawai'ian islands have been the main causal agents in the extinction of at least 22 bird species (30% of the original bird fauna) and are the main reason why 70% of the Hawai'ian plant species are under threat of extinction. More than 1,500 insect introductions have been documented in the continental United States (Sailer 1983). In Hawai'i, introduced species now comprise 28% of the insect fauna (Simberloff 1986). Extreme care should be taken at all times not to introduce exotic species.

Ecological constraints

Every species is unique and irreplaceable, and they play different ecological roles

Biodiversity is not a renewable resource — at least not on a time scale that matters to humans. One can ill afford to lose a species from a community, because we do not know what role it may be playing and what changes its disappearance will engender. Extinction is forever.

Species can still be extant, but be so reduced in number that they can be said to be ecologically extinct — they no longer play the role in the community that they used to. The American bison, for example, while not extinct in North America is for all intents and purposes ecologically extinct today. Following the breakup of former USSR, poaching has become rampant in Siberia and the Siberian tiger is nearing biological extinction — already it is ecologically extinct. Only an immediate and concerted effort from Russia and from foreign financial backers can bring it back. Managers must be concerned not only with keeping species from becoming biologically extinct, but also with keeping them ecologically extant. In either case, the conservation of any given species is much cheaper before it has reached the stage of becoming critically endangered.

Because of the unique ecology of each species, management should ideally be fine-tuned to the ecology of each focal species explicitly. The needs of individual species will depend on such things as their home range size or territory size, their population density, movement patterns (migration patterns), the magnitude and variation of population growth rates at different densities, the biology of critical species on which they depend or interact with in other ways, the spatial distribution of individuals, its degree of clumping and the natural patch structure in its environment, and the importance and variation of extrinsic factors such as disease and environmental variation on its population dynamics.

Because the above information is usually not available, and will require time and money to obtain, various substitutes have been suggested and tried, depending on the management goals and the scale of operations. The simplest and most general tool is to establish and protect reserves that are large enough that the species in them do not require detailed management. Because we typically do not have adequate knowledge about the critical species interactions in the community or communities we endeavor to manage, the prudent course is to protect areas that are abundantly large enough to preserve the species in the community that requires the largest area to survive within the reserve system. Such **umbrella species** are often large top-predators, seasonally migratory species, or extreme habitat specialists.

Organisms occur within specific ranges of environmental conditions determined by biotic and abiotic factors

The kind of environment where an organism lives is its habitat. The limits (for all important environmental variables) within which an organism can live and reproduce is its niche. Biogeography is the study of species ranges and geographic patterns of species distributions. Many species have very small ranges — they are local endemics. Centers of endemism are areas where we can find high concentrations of species that are found nowhere else and probably originated there. EX: Many centers of endemism have been identified in South America (Figure 2), associated with what are thought to be Pleistocene forest refugia. The glacial periods of the Pleistocene were drier and cooler than today, the Amazon Basin was primarily grassland and savanna habitat, and the forest is believed to have retreated to isolated patches which today are particularly diverse and harbor unique faunas. Mountain tops are also likely refugia for many faunas during periods of warmer or drier climates. Such isolated refugia were probably foci for local speciation as well as havens for species that would have gone extinct elsewhere. Other explanations for the Amazonian refugia have been discussed recently (Bush 1994).

Figure 2. Pleistocene forest refugia in tropical South America (after Prance 1973). During dry periods of the Pleistocene, the forests of the lowland neotropics retracted into fragmented forest isolates. Forest species survived in these isolates, and speciation rates were high given the geographic isolation of the patches. Today, these patches correspond roughly to centers of high endemism — biodiversity "hotspots". Recent studies have suggested the existence of more than 40 such refugia in this region (Brown 1987).

food chains and food webs

The trophic connections (who eats whom) in a community is a food web. Because every animal loses energy as heat, energy transfer between trophic levels is imperfect. As a rule of thumb, only 10% of the energy available at one level is transferred to the next. Consequently, it takes a large amount of resources at the producer level to support a predator at the third or fourth trophic level. Species higher up in the food chain are scarcer, and often have to roam over large areas to support their habits.

communities

Although foodwebs are quite complex, they only contain trophic interactions. Species interact directly and indirectly in a network of **competition**, predation, **mutualism**, **commensalism**, and parasitism. Species interactions are obligate, if they depend on one another for survival. For example, many parasites and pollinators are host specific. Specialists are more vulnerable to changes in their environment than are generalist species. Their population densities tend to fluctuate more in response to changes in their critical community links. Tropical forests differ from temperate forests in the important role animals play in seed dispersal; changes in the abundance and diversity of mammalian seed dispersers may have large and unexpected consequences on the forest. Determinants of species diversity in communities include habitat heterogeneity, the amount time since last disturbance, diversity of particular taxa, historical factors, etc. The relative role of species interactions and accidents of history in determining species composition of communities is still somewhat unclear.

<u>There are several kinds of rarity</u>
Most species are rare. We can distinguish at least seven kinds of rarity, based on the species' geographic range, habitat specificity, and local population size (see Rabinowitz et al. 1986). For instance, rare species can be a) widely distributed, with broad habitat specificity but always small local populations, or have a narrow geographic range, restricted habitat requirements, but with some large populations (see Table 1). The Haleakala silversword is an extremely restricted endemic composite plant which is found only in the "crater" of Haleakala volcano on Maui. Approximately 47 000 individual plants exist within this tiny range, but it clearly is a plant that can be considered rare and which warrants special vigilance.

Table 1. Seven types of rarity.

WIDE GEOGRAPHIC DISTRIBUTION
broad habitat specificity, local populations small everywhere
restricted habitat specificity, population large somewhere
restricted habitat specificity, population small everywhere (may not exist)

NARROW GEOGRAPHIC DISTRIBUTION
broad habitat specificity, population large somewhere
broad habitat specificity, population small everywhere
restricted habitat specificity, population large somewhere
restricted habitat specificity, population small everywhere

(after Rabinowitz et al. 1986)

The "classic" rare species are endemics with small ranges and restricted habitats — narrow geographic ranges, restricted habitat specificity and always small population sizes where they occur. These species tend to be endangered and require protection. Different kinds of rarity demand different management approaches. Among the most important information needed to determine management options for a given species are how widely it is distributed geographically, what its habitat requirements are and how abundant that habitat is regionally and locally, and how large local population sizes are.

Some species may be locally rare, but globally common. Others may have a single or a few larger populations elsewhere. Such populations may be managed for particular political, economic or moral/esthetic reasons or for biological reasons. They may form a distinct subpopulation which contributes greatly to the overall genetic diversity of the species, or they may play an important role in the natural community locally.

Table 2. A species may be rare because

its habitable areas are rare
its habitable areas remain habitable for too short a time
competitors, predators or parasites reduce population below the level set by resources in the habitable areas (particularly predation or displacement by humans)
its habitable areas are small
some habitable sites are beyond its range of dispersal
its resources are present only in small amounts or in low densities
its genetic variation narrowly limits the range of areas it is able to inhabit

(after Begon et al. 1990).

Species and communities exist in a matrix of regional and even global processes that must be maintained

Ecological communities are the products of many generations of inter-species interactions, feedback mechanisms, particular disturbance regimes, and interactions between biotic and abiotic components of the environment. Individuals are adapted to making a living in these communities, even temporally shifting communities. Changing the conditions under which the species evolved invariably causes changes in the community, many of which may be amplified by (potentially unknown) species interactions and many of which may come as a complete surprise. The general advice to a tinkerer applies: if you don't know what you are doing, don't mess with it.

Succession is the sequence of community changes following a major disturbance. Some species are adapted to rapid colonization of disturbed sites. Others rely on greater competitive ability to eventually displace the pioneer species. An early view of succession was one of a highly ordered sequence of species assemblages moving towards a sustained climax community, determined by climate and edaphic conditions. In the more recent view, there is more than one possible climax community. The order of recolonization can be highly variable and determined by chance events. Disturbances of different kinds and sizes may have different recruitment patterns. Mahogany, for example, seems to require large landscape level disturbances (hurricanes, floods) to recruit successfully. Some disturbances can carry the ecosystem into quite different domains of attraction. Human disturbances often differ from natural disturbances in that humans often remove nutrients from the system.

Competition between individuals of the same species (intra-specific competition) occurs because resources used by one individual is no longer available for another. This induces density dependence in the population dynamics of the species. The carrying capacity of a habitat area is the limit set to the population size of a focal species by the availability of resources. Resources may be broadly defined, to include for instance the number of available nesting sites or the number of defendable territories. All populations are ultimately density dependent; only populations that are still small compared to their eventual carrying capacity can be reasonably well described as density independent — but only in that relatively short period of exponential growth.

Individual populations can exhibit a range of population dynamic behaviors, from relative stasis, through regular multi-annual cycles of different periodicity, to deterministic chaos and population crashes. Transition between these regimes can be related to the shape of their density dependence. Threshold responses in population dynamics are poorly understood. Allee effects are one set of phenomena that lead to such thresholds. They occur when populations growth rates are reduced at low densities, and tend to lead to further population declines. They may be related to the problems of finding appropriate mates at low densities, increased vulnerability to predation. They are often related to behavioral mechanisms and social interactions. Such abrupt declines in populations may be difficult to predict because the problem may well go undetected until a critical threshold is reached. Catastrophic population collapse has been documented in a number of real-world situations. EX: the passenger pigeon was once the most numerous bird in the world. Before this century, clouds of pigeons would occasionally blacken the skies of the eastern United States for days. Its habit of communal breeding has been implicated in the birds demise. Once hunting had brought its numbers down below a million or two, they did not breed successfully. The last passenger pigeon, Martha, died in captivity in 1929 (two species of obligate ectoparasites, the lice *Columbicola extinctus* and *Campanulotes defectus*, accompanied her into oblivion).

Inter-specific competition occurs when different species use some of the same resources. A variety of mechanisms are involved in allowing competing species to coexist. A **guild** is group of ecologically similar species that may exhibit some level of functional redundancy in the community. Relative abundance within a guild, of rainforest trees for example, may be primarily random. Because of density dependence, we may see some density compensation when individuals are removed from the community — enhanced growth due to release from competition (this is essential in harvested systems). If two species compete, one may benefit from the harvesting of the other. A population increase in the unharvested species may reduce the harvested species' ability to compensate for the harvesting mortality.

Communities are dynamic, not stable entities. At most, we can say that communities change in a phase space with different basins of attraction. Complex systems have multiple steady states. The internal dynamics of habitat patches are important in maintaining overall diversity.

Keystone species are species that play a pivotal role in a given community, either as food for others (perhaps by producing fruit at a time of year when few other species are fruiting), through their effect on vegetation or essential abiotic processes, by a significant regulatory function on other species, or through critical mutualisms. Because of their role in critical links of other species' environment, keystone species are critical to ecosystem integrity and community dynamics. Consequently, effective management has to preserve the population densities as well as the viability of the keystone species. However, it can be difficult to identify keystone species without an actual removal experiment or at least a thorough understanding of the natural history of candidate species. Furthermore, one can never be certain that a community does not contain a keystone species that has not been identified as such.

EX: Fig trees are keystone species in many tropical forests because they produce copious fruit at a time of year when other fruits are scarce. Thus, they sustain an entire community of frugivores. The figs themselves depend on specialist pollinators and other mutualists. In long-term lake acidification experiments Schindler (1990) found a great deal of redundancy in the phytoplankton, such that primary productivity was not affected by moderate acidification of the lake. When acid-sensitive species disappeared they were replaced by others in the same functional niche. But there was much less redundancy among the species on the lake bottom. Food chain structure and function of the whole lake were affected by declines in certain crustacean species, because no species were present that could replace them as an important food chain link between primary producers and fish. That is, these crustaceans proved to be true keystone species (Odum 1993).

Almost every species is dependent upon other species for food, habitat structure, pollination, seed dispersal, and other necessities. Direct interactions are relatively well understood, but indirect effects are not. The loss of one species will invariably cause the extinction of others. The importance and extent of such cascade effects and synergistic interactions are almost entirely uninvestigated. Yet they are potentially the biggest factor of all. Because ecological systems contain interactions and mechanisms that may amplify effects of a local perturbation in nonlinear ways that are unknown, ecologists and habitat managers must proceed with much more caution than physicists and engineers. Engineers also build in large margins of safety in their bridges and dams, yet they deal with simple systems with largely linear mechanisms without interaction terms (or at least linear interaction terms). Ecologists and habitat managers are confronted with dynamic systems with highly non-linear responses and non-linear interaction terms, the shape and details of which are largely unknown and largely uninvestigated. Managers will be well served by taking the time and bearing the expense of investigating critical ecosystem and community components in detail and determining the extent and functional form of critical interactions. EX: Nile perch was introduced to Lake Victoria in an effort to establish a new fishery. It has since proceeded to exterminate dozens of endemic species of cichlid fish — fully 50% of the 400 cichlid species in the lake have been exterminated. Many other fish have disappeared from African lakes after the killing of hippos. Hippo excrement had supplied nutrients to phytoplankton, which in turn used to feed the fish. Without the hippos the fish stocks declined drastically. Similar examples are numerous (Yablokov and Ostroumov 1991).

Indicator species

Indicator species are like the canaries in the mines of old. The supposition is that certain species are particularly susceptible to various environmental changes, and can therefore serve as an early warning signal if something is amiss. Some species may also serve as indicators of areas with high biodiversity. EX: frogs and certain other amphibians are particularly sensitive to pollutants since their skin is highly permeable. Their eggs are also very sensitive to ultraviolet radiation. There has been a dramatic global decline in amphibian populations. Their decline has been linked to ozone depletion, habitat loss, and pollution. Butterflies are better studied than most other taxa. In the Amazon, high butterfly diversity seems to correlate well with high diversity of other faunas.

In ecological systems, some resources have no substitute

Water, air, soil (nitrogen, oxygen, potassium, etc.), sunlight, etc. have no substitutes. It takes 500 years to generate 1 inch of topsoil. During the last 40 years nearly one third of the world's arable land has been lost to erosion (Pimentel et al. 1995).

Some species are adapted to a particular resource, a specific tree species on which they feed or lay eggs for instance, for which there is no substitute (on ecological time scales). Some species rely on others to disperse their seeds, pollinate their flowers, digest their food, etc. There are tree species on Mauritius that have not produced a seedling in over 300 years because they depended on the dodo to pass their seeds through its digestive tract before they could germinate. These species are the living dead.

Some ecosystem changes, once started, are hard to reverse. EX: When trees are removed in some habitats, they revert to grasslands. Grasslands usually burn on a regular basis and suppress the reestablishment of trees. The community has shifted into a new domain (basis of attraction) where it may remain until perturbed by some other large environmental change.

<u>The true cost of any project includes disruption of "free" ecosystem services</u>
Each year, 75 billion metric tons of soil are removed by wind and water erosion, most of it from agricultural land. The cost of soil erosion has been estimated at $40 billion every year in direct damage to agricultural lands and "indirect damage" to waterways, infrastructure, and health in the United States alone, and nearly $400 billion worldwide.

Almost every large city in the world is located on large bodies of water that provide natural waste treatment facilities. These free sewers are becoming overloaded, and wont be free any more when their capacity to assimilate waste is destroyed (Odum 1993). Bees pollinate 30 billion dollars worth of crops every year in the United States alone (David Pimentel). There is no technology to replace this service.

The biological resources that shelter biodiversity have value: clean air and water, forests. Forests supply 75% of fuel to poor people of the world. On the larger scale natural ecosystems purify water, rid the air of carbon dioxide and recycle oxygen, regulate climates on local, regional, and global scales, recycle nutrients, break down pollutants, and maintain ecosystem conditions within the narrow bounds in parameter space under which life as we know it thrives.

Water is chronically underpriced. We also underprice grazinglands and timber. The destruction of the everglades is fueled by subsidies to the Florida sugar industry and protectionism that makes the citizens of the United States pay three times the global market price for sugar. Using, rather than disrupting, "free" ecosystem services makes management efforts, whether for extraction or conservation, more effective, sustainable, and robust (Jordan 1995).

<u>Natural systems confer stability within certain basins of attraction</u>
Over millions of years species have adapted to utilizing just about any resource that was available in any amount. This includes the waste of other species, debris, other species, resources that other species produced specifically to entice others for their services, parts of other species that were either essential to the individual, that it wanted to get rid of, or that it wanted dispersed, and a variety other ordinary and unusual resources. Everything is a resource to someone else. This utilization leads to a) substances do not build up to the point where they become a problem, and b) negative feedback loops are introduced. a) contributes to a livable environment for all. b) provides checks and balances that lead to stability within a domain. Negative feedback loops stabilizes systems as long as the rates of change are moderate and the functional forms of the feedback are not too steep. Species that destabilized systems would either go extinct themselves or drive the system into a new domain where they were no longer destabilizing.

It is important to note that this stability "evolved" over thousands and millions of years. Furthermore, new occurrences can abruptly change the system away from one basin of attraction into something completely different. "Stability" does not imply a point equilibrium. Natural systems are highly variable over time, sometimes changing abruptly in response to an unusual environmental perturbation, sometimes exhibiting regular oscillations with periods from days to decades, sometimes fluctuating erratically either through stochastic events in small populations or through deterministic chaos. Stability simply infers that the system is regulated within certain bounds, as long as a major perturbation does not shift the system into a new domain. On ecological time scales the only truly stable state is extinction.

It is not entirely clear whether species rich systems are more robust than species poor systems, or more resilient, or even less variable. Some experiments suggest that species rich systems may be less vulnerable to perturbations and may return more rapidly to the predisturbance state than relatively depauperate systems. For instance, an experiment in Minnesota showed that species rich grasslands were more resistant to a severe drought and returned more quickly to pre-drought biomass than did impoverished communities (Tilman and Downing 1994). Stands of native prairie had more resilience than three different successional stages. The alternative hypothesis (the species-redundancy hypothesis), that many species are so similar that ecosystem function is independent of diversity if major guilds are present, was rejected. It is clear that natural ecosystems have developed a kind of stability within particular domains by trial and error over a long time, and that those systems that remain are ones that possessed this kind of stability. We also know that large perturbations can alter such systems to the unrecognizable, and that we have no way of telling what they might change to once that happens.

Unfortunately, we generally do not know what the critical links in ecosystems are — links that if broken may cause nonlinear cascade effects throughout the system.

The ecological world is finite

As all populations have a limited amount of space and resources available to them, every population is ultimately density dependent. Density dependence has profound effects on population and community dynamics that cannot be ignored except in the very short term in peculiar circumstances when population densities are very low. Species ranges are limited by biotic and abiotic factors, such as temperature, humidity, salinity, competition, etc. There is no such thing as perpetual growth.

Another limit to global carrying capacity is the incident solar radiation, from which all food is derived. Global net primary productivity is the net growth of organisms that utilize this solar radiation directly through photosynthesis (the total energy accumulated by plants during photosynthesis). It is roughly equal to the total food supply of all animals and decomposers. Almost 40% of all net primary production on land is presently directly used, coopted, or foregone because of the activities of just one species — us. While only about 4% of net primary production is used directly by humans and domestic animals, some 34% more is co-opted by nonedible production such as lawns or nonedible portions of crops or is destroyed by human activity, such as tropical deforestation and desertification (Vitousek et al. 1986). Since the majority of species (possibly more than 90%) live on land, the appropriation by humans of 40% of terrestrial net primary productivity shows why there is an extinction crisis (Ehrlich and Wilson 1991). It also makes it difficult to envision how we could accommodate a doubling of human population size in the next 35 years or so, let alone the five to tenfold increase in global economic activity that the Brundtland Report calls for in that period to meet the demands of that exploding population.

Scale is important

Different species operate at different spatial scales. Natural communities exhibit patchiness and clumping in distribution patterns at many different spatial scales. Ecological processes interact at a diversity of scales, and a diverse community requires a diversity of spatial scales. Density dependence and species interactions are exhibited differently at different spatial scales.

Every problem must be dealt with at the appropriate spatial scale, so analysis begins with identifying the appropriate spatial scale. The system must be explicitly specified: the temporal and spatial scale, boundaries, scope of the problem, etc.

In a large, continuous tract of wilderness each species is free to function at its own spatial scale. When populations become isolated in small habitat patches surrounded by development, ecological processes may be interrupted and community interactions perturbed. In connected reserve systems, each corridor and the connected refuges can be constructed at the appropriate spatial scale for only a few species.

Ecological time scales range from months to decades. Evolutionary time scales range from years to millennia, or hundreds of millennia. Both are perhaps best thought of in generations, or inter-birth intervals, of a focal organism. Different species operate on different temporal scales. Ecological systems take time to adjust after a perturbation. Ecological time scales are short compared to evolutionary time scales; species must have time to adapt to changes.

Since ecological and evolutionary timescales are typically much longer than economic turnover times, and natural populations and communities must be maintained in the long term, economic discounting is not appropriate in analyses involving their management. The ecology is the boundary within which economical analysis and policy must operate. In ecology, long term consequences are important. Because of discounting, standard economic theory ignores just about everything further than about ten years into the future. Since ecosystems must be maintained indefinitely, ecological constraints must define the boundaries within which economists must operate. The future is just as valuable as the present.

Biological growth rates are often low

This is especially true in the most threatened and sensitive biomes (mature forest, tundra, coral reefs). It is also especially true of large vertebrates which today are often critically endangered or ruthlessly exploited: rhinos, sharks, tigers, pandas, condors, whales, sea turtles and tortoises, crocodilians, etc. To harvest sustainably extraction rates must be lower than replacement. Sustainable harvesting requires a system of extrinsic regulation or structural checks since with only economic considerations the rational operator would harvest the resource to extinction any time the discount rate exceeds the intrinsic growth rate of the harvested population. On a national scale, a lowering of real interest rates should be a powerful tool in aid of sustainable management of natural populations.

Safety margins must be built in.

The dominant cause of species loss is habitat loss

The loss of species is expected to accelerate markedly in response to fragmentation when a large part of the habitat has already been cleared.

Communities change as they become isolated in smaller habitat remnants

One of the strongest empirical generalizations in ecology is the relationship between the area of an island and the number of species on it. In this context, islands can be any landscape feature that is isolated from other features like itself by a sea of something else: oceanic islands, a nature reserve in an otherwise developed habitat, a stand of trees in a sea of wheat, a rainforest remnant surrounded by slash and burn agriculture. Plotting the logarithm of the number of species on islands versus the logarithm of their area, we can usually fit a straight line to the data and get a regression which accounts for a very large part of the variation (Figure 3). This phenomenon is usually referred to as the species-area relationship. Continental species-area curves often have slopes of approximately 0.15-0.2, though they may be much steeper depending on the isolation of the islands, the fauna or flora in question, and the spatial scale. Floras and faunas that are more isolated (e.g. species on oceanic island) tend to have much steeper species-area curves. Consequently, habitat patches that become isolated will lose species, more species the smaller they are. The consequence of this is that a 90% reduction in area leads to something like a halving of the surviving number of species. A 90% reduction of available area may seem like a lot, but consider that only 1% remains of Brazil's Atlantic rainforest, or consider how little remains of the old-growth forest in the United States or Western Europe.

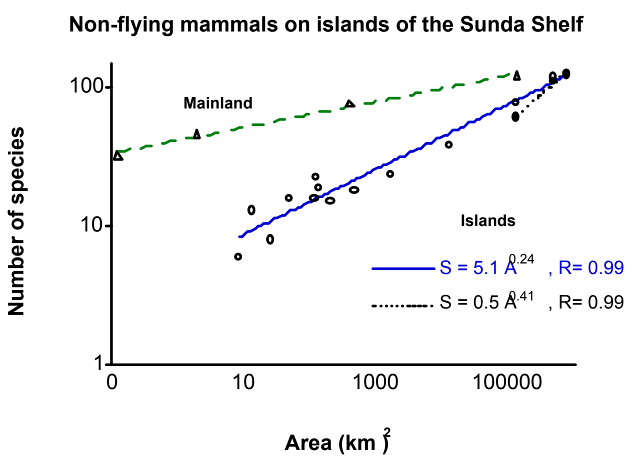

Figure 3. Species-area curve: the number of species in a focal taxa, as a function of area (data from Heaney 1984, 1986). Open circles represent all species of non-flying mammals presently on islands of the Sunda shelf, which became isolated from the Malay peninsula mainland at the end of the Pleistocene (about 10 000 years ago). Closed circles represent only native species (excluding introduced species), on Borneo, Sumatra and Java. Triangles represent the number of species in areas of the Malaysian peninsula mainland. Species area curves for habitat areas that are not isolated from other tracts of similar habitat are not nearly as steep as they are for habitat isolates like islands. When nature reserves become isolated from similar natural habitat — they become islands in a sea of inhospitable territory — they lose species. Small reserves lose more species than large reserves. The number of species lost are represented by the difference between the number of species in the isolate and the number of species in a comparable area on the "mainland". Peninsulas are often relatively depauperate — perhaps due to their semi-isolation — and the island faunas are inflated by introduced species, suggesting that species loss from isolates will often be greater than indicated.

It is on the basis of this species-area relationship that ecologists have calculated that perhaps as many as 270 species are going extinct world wide every day, or about 100,000 species per year. These numbers are obtained by estimating the number of species present in tropical rainforests of the world, and estimating the rate of tropical deforestation (perhaps 1.8% of the world's tropical rainforests are burned, bulldozed, or chain-sawed every year). Unfortunately we don't even know to the nearest order of magnitude how many species there are in the world. Presently, about 1.6 million species are described by science. Estimates of world-wide species richness range from 5 million to 100 million, with the vast majority of these species occurring in the tropical forests. The estimation techniques used are very crude. Nevertheless, species area curves can yield simple estimates on how many species will disappear within a habitat type at a particular site if its overall area is reduced. A recent estimate suggests that 3 species are lost every hour.

Several factors contribute to the species area relationship. One is the great importance of habitat heterogeneity in species diversity. Different species occupy different niches and live in different kinds of habitat. An area with both savanna and forest will harbor both forest species and savanna species, and hence a greater number of species than an area with only forest. Larger areas tend to cover more habitat heterogeneity, more patches of different kinds of habitat, and contain more species than small areas. Habitat heterogeneity is also important because it may allow potential competitors to coexist by specializing on different resources, or it may supply partial refugia for prey species so that predators and prey can persist together in the same environment. Habitat heterogeneity plays an important role in speciation, by allowing populations of the same species to be spatially separated and experience different environments.

Complex environments provide more opportunities to specialize and provide resources for species that are adapted to special conditions. That is why a mono-culture, for instance a tree-farm, harbor much fewer animal species than a complex community like a lowland rainforest where hundreds of tree species may coexist. Diversity begets diversity. Complex communities have also shown themselves to be much more robust against pest-outbreaks, perhaps due to the host of natural predators of such pests that complex communities harbor. Of course, outbreaks on a scattered resource are necessarily on a smaller scale, and specialized pests have greater difficulty in sustaining a population explosion on a scattered resource.

The other important factor responsible for the species-area relationship is extinction in small populations. According to the theory of island biogeography (MacArthur and Wilson 1967), the number of species on islands, be they true islands or terrestrial habitat islands, is determined by the equilibrium between species immigration and species extinction in situ (Figure 4). The fate of individuals are partially stochastic — they are subject to random events. Populations fluctuate over time, and small populations are more likely to go extinct because they are more susceptible to random events. In small habitat isolates there are room for smaller populations, and these have higher extinction rates than larger populations in larger areas. Isolated habitat patches have low rates of immigration from similar habitat types. Consequently, small and isolated habitat remnants harbor fewer species.

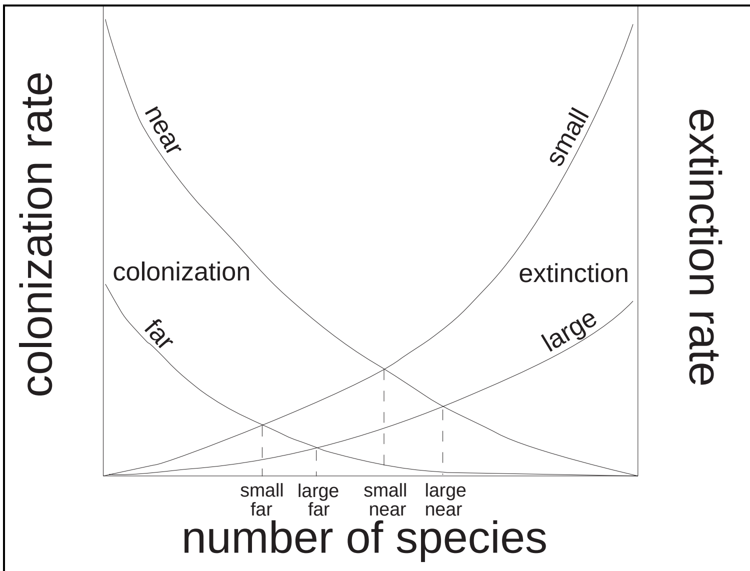

Figure 4. The equilibrium model of island biogeography (after MacArthur and Wilson 1967). Isolated islands, or reserves, have lower colonization rates than less isolated islands. Small island have higher extinction rates than large islands, because they have smaller population sizes. A dynamic equilibriu between colonization and extinction determines the number of species. When islands or reserves become isolated, and/or reduced in size, it may take a long time before a new equilibrium is established at a lower number of species. Isolation may also affect the extinction rate since immigrants of a given species may postpone its extinction. This is known as the "rescue effect" (Brown and Kodric-Brown 1977).

Nature reserves are often such small and isolated patches. Those that are not already entirely isolated from other similar habitat areas, are in ever increasing danger of becoming so in the near future. Small areas also contain less environmental variation and fewer niches for different species. Hence the need for large nature reserves. Some species may exist only in a single valley, or a single forest remnant, and nowhere else in the world. If that single patch is disturbed, the species may be globally extinct.

Genetic stochasticity and inbreeding is also a problem in small populations. In small populations, the inbreeding frequency increases and genetic variation is lost when individual genes by pure chance happen to not be passed along to the next generation. Inbreeding lets deleterious genes become expressed more often, and the population is weakened. Loss of genetic diversity makes the population less robust to environmental changes and reduces the ability to adapt evolutionarily.

It may not be a good idea to make general rules of thumb about how large reserves need to be. Some studies suggest that even the largest national parks of East Africa, ranging from 10 000 to 50 000 square kilometers, may lose many of their large mammal species rapidly when they become isolated from other habitat areas (see Meffe and Carroll 1994, Burkey 1995a). If forced to give a simple rule of thumb for a minimum reserve size, I would say that a reserve should be large enough that the most vulnerable large vertebrate has a population size within the reserve of more than 500 individuals. If this focal species suffers high losses to predators, the minimum population size must be larger. Modifications could be made if the population in the reserve will not become isolated from healthy populations elsewhere — though unless our priorities change considerably in the coming decades, all reserves are likely to become completely isolated from other habitat areas before long. We should assume that the only natural habitats left in the future may be those protected inside nature reserves. This "rule of thumb" assumes that populations are safe within the reserve and do not need to wander into adjacent areas where they are not safe. If populations are subject to human induced mortality like poaching, environmental toxins, or livestock diseases, minimum population sizes should be much larger. If the population size of the most vulnerable species is artificially low (due to poaching for instance) the area should be large enough that it would have room for at least 500 individuals when they are fully protected. In this case, another population should be protected elsewhere or another protected population established somewhere else as well.

Shorter lived species will need larger minimum population sizes. Invertebrate species and populations with highly variable population sizes will need much larger minimum population sizes. In addition to maintaining reserves large enough for viable populations of the most vulnerable species, special consideration must also be given to species that occur nowhere else. These should be subject to their own viability analyses. Smaller reserves will require expensive management efforts and monitoring. Small populations within any reserve, particularly small, short-lived species (like annual plants) and species that are subject to large fluctuations in numbers (like many insects and rodents), must be monitored carefully and may require intensive management. Habitat specialists, like wood boring or host-specific necrophilic insects, must be allowed large enough areas that they can always find enough of their critical resource (which may be patchily distributed), to maintain viable populations.

Because species tend to go extinct in a predictable or regular order when the area available to them is reduced, a set of small reserves in the same biome will tend to preserve the same set of species and the large predators that have large area requirements will be lost from the whole reserve system. Therefore, it is usually better to have one large reserve than several small (Figure 5). Computer simulations and simple laboratory experiments suggest that a species will usually have higher survival chances in a single large reserve than in a set of small reserves of the same overall size (Burkey 1995b). This seems to be true for most species, and on most spatial scales. One potential exception is situations where disturbances like forest fires or diseases play an important role. Then it may be advantageous to have several protected populations in partial isolation so that such events do not wipe out the entire species. There are, however, may reasons why habitat fragmentation should be avoided. Top predators, like jaguars and pumas, living at the top of the foodchain need large territories to find enough prey. When the population density is so low, reserves must be large to avoid extinction due to demographic or genetic stochasticity.

Wherever humans reduce the area available to the original inhabitants of the area, they create habitat edges between the original habitat remnant and the new anthropogenic habitat. Small and fragmented habitat remnants, or reserves, have more edge in proportion to their area than large, continuous remnants. Different species thrive in the new edge habitat. Species that invade the edges often come from the new habitat that now borders on the old. They often displace the species of the original habitat. They also tend to alter ecological processes like predation, recruitment, and the outcome of competitive interactions. The new edge species often take a heavy toll on the original inhabitants through nest predation or parasitism, seed predation, herbivory, and similar processes. The fact that small, fragmented reserves house such edge species is no advantage, since these are species that manage quite well even in the absence of reserves. They are the species that tend to thrive in disturbed areas and areas modified by humans — areas that are in abundant supply in today's world. On the contrary, they tend to displace the sensitive habitat interior species that really do need protection and management. The local micro-climate changes in habitat edges. In rainforest habitats, the edges are hotter and dryer than the forest interior, and tree falls are much more common near forest edges — creating "moving edges" as trees on the edge fall down and create a new edge further in. Furthermore, areas with high edge to area ratios are more accessible to poachers, loggers, and landless peasants. One of the most apparent features of satellite images of many habitats are the widespread and continuing encroachment around every little road that is built through a previously undeveloped tract of land.

Roads form movement barriers for numerous species, even animals as large as black bears (see Noss and Cooperrider 1994). When a new road is constructed, species that hesitate to cross roads or to go near roads are effectively fragmented into smaller demographic units that are much more vulnerable to extinction. Edge effects have been demonstrated near even very small roads, in different kinds of habitat around the world (Burkey 1993). Roads are also a major mortality factor. For example, roadkill is the leading known cause of death for all large and medium-sized mammals in Florida — with the exception of white-tailed deer, but including the critically endangered Florida panther. Studies in Wisconsin and Minnesota indicate that wolves cannot maintain populations where road density exceeds 0.9 miles per square mile. They do not generally avoid roads, but following roads brings them into contact with people who shoot them. Similarly, most grizzly bears die near roads, though they tend to avoid areas near roads.

Nature reserves must be large enough to preserve the ecological processes that the flora and fauna depend on. For instance, one should strive to protect the entire catchment area of a critical watershed. Critical migration routes should be protected inside the reserve, or reserve system.

Regrettably, nature reserves are often not situated where they would be most valuable from a biological perspective, but where humans have least economic interest in the land.

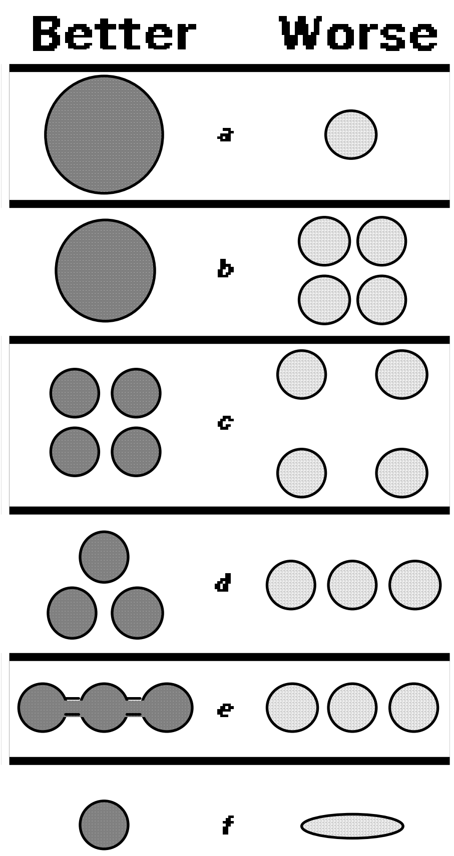

Figure 5. Recommendations for natural habitats conservation (after Diamond 1975 Protecting a large area is better than protecting a small area. Under most circumstances, species will be less likely t go extinct in a single large area than in a s of small areas which together cover the same amount of land. Dispersal between habitat remnants will enhance population persistence, therefore habitat patches sho be close together and preferably connecte with dispersal corridors. Edge effects are usually detrimental to the kinds of species that need protection, so one should always strive to minimize the edge to area ratio of the reserves system — by avoiding long narrow reserves, and minimizing the degre of habitat fragmentation.

All areas are not equal, and all species are not equal. Predators need larger areas than herbivores.

Box 2. Difficulties of managing migratory species — wildebeest migrations

The seasonal migration of wildebeest and other large herbivores is a major factor in the ecology of east African savanna habitats. The migration of wildebeest in the Serengetti take them across the border to Kenya, where fortunately, they find protected habitat in Masai Mara National Park. Botswana and other southern African countries have painful experiences of what can happen when gnus and other large herbivores find their traditional migration routes cut off by cattle fences. By 1987 more than 3000 km of fences had been constructed in Botswana to separate wildlife from cattle. Wild herbivore species can be carriers of hoof and mouth disease, and one perceived a need to keep wildlife from competing for grazeland with the cattle. In 1963 more than a million wildebeest started the wandering north towards the Okavango. They were stopped by a 300 km long fence which forced them eastward towards an area without food or water. 300 000 wildebeest succumbed to thirst and lack of food. Similar tragedies have occurred regularly since. In 1983 52 000 out of a population of 80 000 gnus died near Lake Xau. In 1987 only 260 gnus were registered in central parts of the Kalahari (Ross 1987).

Large predators need larger areas than small predators. Some areas have high concentrations of species, of which many may not exist anywhere else. For example, as much as 12% of all bird species on earth have been found between 400 and 4000 meters in the headwater region between the Río Tambopata in Peru and the Río Alto Madidi in Bolivia (Parker and Bailey 1991). In some areas, local population of some species may only persist because they receive the surplus from adjacent areas. If a reserve is established in such a "sink", without protecting the "source", the species will go extinct locally. When a tract of habitat becomes isolated, the fate of organisms therein depend on whether they are self-sustaining populations in the patch itself or whether they used to rely on dispersers from adjacent areas for persistence. Sources can be used to economic advantage for instance by establishing marine reserves which may act as sources for fisheries in surrounding areas, adding resilience in an otherwise sensitive harvesting regime

The species diversity depends on ecosystem processes that must remain intact. EX: Elephants modify the habitat where they occur from forest or forested savanna to grassland. Grasslands are important habitats for other species, but not for the elephants, which must keep moving to find areas with sufficient tree cover. Elephants play a very important role in the savanna community, but if they become isolated in too small an area, they will change the community away from their own optimum. The successional process itself will be disrupted; that can have large, often surprising, perhaps irreversible repercussions within the ecosystem. If it is impossible to protect a large enough region in a single reserve, at least one should establish dispersal corridors to other protected wilderness areas such that animals can seek resources there when they are not to be found within the reserve, and so that the reserve can get recolonized from without if a species goes extinct locally. How well such corridors function in practice is not well known, and this will probably vary from one species to another.

Nature reserves have not been isolated long enough, or are still not entirely isolated from other natural habitats, to tell how many species they can preserve over time. For instance, about 50% of the national parks and reserves in the African savanna zone are smaller than 500 square kilometers. Assuming that a few hundred individuals are needed for a population to survive in the long term, very large areas (>10 000 km^2) are required if the large carnivores are to survive. It is possible that even the largest reserves — Selous, Salonga, Namib desert, Kafue, Etosha, Tsavo, and Kruger — are too small to preserve large predators and important mega-herbivores in the long term. Even large reserves experience problems with overpopulation of certain species, low population densities (especially in dry regions), cattle, etc. Serengeti would be too small for the wildebeest if it were not contiguous with Masai Mara on the Kenyan side of the border.

This is not to say that small reserves are without value. Wisely placed, small reserves may play an important role for some species, especially if they form part of a network of reserves where species can persist in a **metapopulation** structure. A large region with many partially independent communities will still have some turnover in species composition within communities over time, while the species persists in the region as a whole. This metapopulation structure makes it so important that the linkages between communities be maintained. The appropriate size for a nature reserve may hinge on the concept of minimum dynamic area — the smallest area with a complete natural disturbance regime.

Small reserves may also be important repositories for genetic diversity if they succeed in preserving genetically distinct populations of small species. A reserve that is too small for rhinoceros can be large enough for rhinoceros beetles — provided the habitat does not change too much when large species like rhinoceros and elephants are lost. A reserve that is too small for elephants, is also too small for elephant dung beetles, which need elephant dung to reproduce successfully. Similarly, several Amazonian frog species apparently require for successful breeding persistent terra firma ponds that are made and maintained by wallowing peccaries (Zimmerman and Bierregaard 1986). The consequences of losing a species from a community can be drastic, wide-ranging, and completely surprising. Small reserves are often established because they have uncommonly high biodiversity and are particularly valuable to wildlife, while large reserves simply were deemed as having little value for human usage. They are often located in dry regions with poor soils and relatively low value both economically and ecologically.

Small reserves will require intensive management. Our ability to manage population and communities is limited. The heath hen was originally common in much of the northeastern United States, but by 1870 hunting and habitat destruction had driven it extinct everywhere but on Martha's Vineyard. There it was driven finally extinct by a combination of catastrophic events including a fire, harsh winter, heavy predation by goshawks and a poultry disease. The last one died in 1932 (Simberloff 1988). Last ditch efforts at conservation tend to be disproportionately costly.

Whether a single large reserve can harbor more species than several small reserves depends in part on how much overlap there is between the species compositions of the small reserves. This depends again on the degree of habitat heterogeneity within and between reserves and the spatial scale of environmental variation. This depends again on the size and spacing of reserves. Often the order in which species are lost from a reserve (or island) is highly regular and predictable. As habitat remnants shrink, the same species disappear on all islands, and in the same order. Large species, especially predators high on the food chain, extreme specialists, and widely ranging animals drop out first and soon are not found on any of the small islands (Fig. 6). While it is possible to sample a greater diversity of species by selectively and informedly siting reserves in hotspots of diversity with little overlap between them, there are good reasons to believe that any such numerical advantage may not last long as species go extinct because their population sizes are too low in small reserves.

Incidence functions are often steep, indicating that there may be critical thresholds of habitat area below which the species will disappear rapidly and deterministically. Figure 6 shows the incidence of flightless mammal species on islands in the Bass Straight. The species distributions are perfectly nested — each species is absent on all islands smaller than a critical size and present on all islands larger than that size. For instance, the rat-kangaroo *A. rufescens* and the mouse *P. novaehollandiae* disappeared from all islands and survives only on the Australian mainland. The marsupial "cat" *Dasyurus viverrinus, H. sapiens,* and nine other species survived on Tasmania and no other island. Carnivores are more susceptible to habitat fragmentation than herbivores, large carnivore more than small carnivores, and habitat specialists more than generalists (Diamond 1984). The steep threshold in area requirements for the different species, suggests a strong negative effect of habitat fragmentation and habitat loss on biodiversity.

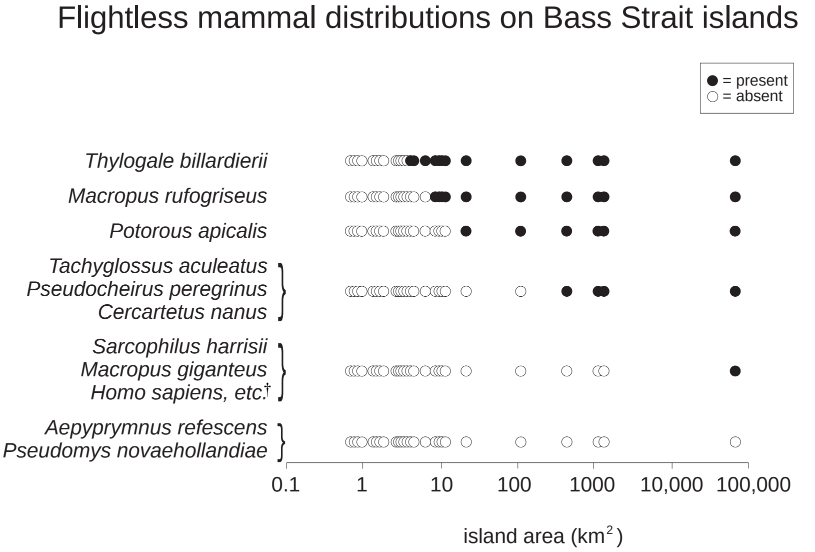

Figure 6. Distribution of flightless mammals on islands of the Bass Strait as a function of island area (adapted from Diamond 1984). This pattern was produced by differential extinction following isolatation from the Australian mainland in the late-Pleistocene (Diamond 1984). There is fossil evidence for the past existence of almost all modern Tasmanian species on smaller islands where they are now absent (Hope 1973). The two species on the bottom line, have disappeared from all the islands, and now persist only on the Australian mainland. † The group on the second line from the bottom also includes Dasyurus viverrinus (the quoll), Thylacinus cynocephalus (the Tasmanian "wolf" — present till at least 1930), Mastacomys fuscus (the broad-toothed rat), and Pseudomys higginsi (the long-tailed rat), Parameles gunnii (the brown bandicoot), Betongia gaimardi (the eastern bettong), and Anthechinus swainsonii (a broad-footed marsupial "mouse"), which all survived only on the largest island, Tasmania (data from Hope 1973).

Large tracts should be protected if for no other reason that they are becoming rare, and the process of fragmentation is essentially irreversible. Time is running out on available options. Reserves should protect natural management units, such as entire watersheds and catchment areas, migratory regions for focal species, and ranges of local endemics. Reserves should be large enough to preserve the natural patch dynamics and disturbance regime of the habitat.

More often than not, the information necessary for prudent management is not available. The rapid pace of environmental destruction and species extinction will limit the feasibility of thorough ecological studies in many ecosystems. What can we do to obtain minimal information quickly and how can we avoid disaster in a limited knowledge environment? If you don't know what you are doing, set off a huge reserve, protect it from encroachment and poachers, and leave it alone. Educating any local human population about the benefits of the reserves can reduce maintenance costs and the need for protective measures.

The special role of tropical forests

While tropical forests, and even tropical moist forests, are quite different from one site to another, certain generalizations are possible in comparison with temperate forests. Tropical rainforests harbor the vast majority of the earth's existing species. Yet they cover only 6% of the global surface. A hectare of moist forest in South-East Asia or South America can contain more than 200 species of trees with a diameter at breast height greater than 10 cm. Invertebrate diversity is the greatest and least well known. Estimates of the global number of arthropods range from 3 million to 100 million species. Small ranges and extreme specialization makes the majority of these species especially vulnerable to extinction. Tropical forests are also disappearing with alarming speed. 18 million hectares of closed tropical forests are cleared each year. Sommer (1976) estimated that 52% of the tropical moist forest of Africa has disappeared. Similar numbers for Latin America and South-East Asia were 37% and 63.5%, respectively. Forest clearing rates increased substantially during the 1980s. Globally, rainforests have been reduced to 55% of their original cover, and roughly 1.8% of the remaining forests are disappearing per year. By the most conservative estimates, 0.2-0.3% of all species in the forests are extinguished each year. If five million species are confined to the forests — a very conservative estimate — then tropical deforestation alone must be responsible for the loss of at least 12,000 species annually. If current rates of forest clearing are continued, one quarter or more of the species on Earth could be eliminated within 50 years, and even that estimate could be conservative (Ehrlich and Wilson 1991).

In spite of the enormous biological richness of the tropical moist forests, this biome is less well known than any other. We know more about certain sectors of the moon than about the heartlands of many tropical forests (Myers 1984).

Tropical forests are not like temperate forests. It would be a great mistake to base management decisions and forestry practices on experience from temperate forests. Tropical forests are often located on lateritic and nutrient poor soils. The great standing crop of vegetation is made possible by very efficient turnover and assimilation of leaf litter and other dead materials. Nutrients are concentrated in the trees themselves, not in the soil. Remove the trees and you remove the nutrients. Some of these nutrients are recovered in the process of slash and burn agriculture, but they are rapidly consumed by crops and leached out of the soil. With land clearing and continuous cropping, the organic matter content of soils of the human tropics declines rapidly, because of continuously high temperatures throughout the year (National Research Council 1993). Rapid degeneration in soil fertility can also occur because of the dependence on nutrient cycling by deep-rooted plants in some soils common in the humid tropics (like ultisols; National Research Council 1993).

The enormous diversity of tropical forests is accompanied by another feature: low densities of individual species. These populations are very vulnerable to extinction in isolated forest fragments. Tropical forests are not very productive systems. The effective assimilation of nutrients is in many species made possible by a symbiotic interaction with fungi; different kinds of ectomycorrhiza. Phosphorous mobilization is another "free" ecosystem service. The interaction between soil microbes and tree is a mutualism which is also a positive feedback mechanism.

Animals play a much greater role in dispersal and recruitment of forest trees in the tropics than in the temperate zone. The frequency dependence in recruitment imposed by seed parasites and predators may also play a determining role in the maintenance of the high diversity of tropical tree species. Without the animals the rainforest would be completely different, and certainly have much lower diversity of tree species.

In unprotected habitats, forestry practices (like selective logging) that are more appropriate to tropical systems may prove more sustainable alternatives to destructive logging and other intensive land uses. These must be tuned to the biology of the species in question. For instance, some tree species (like mahogany) need large disturbances to recruit successfully, in which case a single clearcut in an otherwise intact forest may be better than selective logging. Recruitment conditions for different species are a very critical variable in management of particular species. Many species (for instance Dipterocarps) have massive and infrequent mast fruiting events to satiate seed predators. By synchronizing fruiting with many conspecifics over a large area, the seed loss of individuals are reduced to where they can recruit successfully. Species have evolved this adaptation over millennia. Thinning the species or limiting the population to a small area may shift the present balance to where seed predators could eat all the seeds and effectively block recruitment of the tree species.

There are few if any examples of demonstrably sustainable harvesting of either timber or non-timber tropical forest products. Even in the case of well known products like brazil nuts and mahogany we lack a sufficient knowledge base to design a sustainable extraction system (Boot and Gullison, in press).

Forests influence rainfall patterns. Some tropical forests generate their own rainfall by forming regional weather-cells. Ecological costs of forest degradation include disruption of hydrological processes, soil erosion and degradation, nutrient depletion, loss of biological diversity, increased susceptibility to fires, and changes in local distribution and amounts of rainfall. Economic costs include loss of production potential as soil is degraded, loss of biological resources like food and pharmaceuticals, destabilization of watersheds with attendant downstream effects of flooding and siltation, and at the global level, the long-term impact of deforestation on global climate change.

Unless we understand the factors that govern the structure and dynamics of tropical forests we are unlikely to manage them correctly.

<u>Habitat heterogeneity is important</u>

Diversity begets diversity. Heterogeneity creates opportunities for specialization and niche partitioning. Each species is a resource for other species — often an exclusive resource. Each species has obligate host parasites, mutualists, and commensals that depend on them. Each species is a substrate for evolution. Heterogeneity stabilizes species interactions.

Small is beautiful. A small localized disturbance can add to landscape heterogeneity, while large disturbances reduce it. This is true in agriculture, forestry, fisheries, even hydroelectric projects. Heterogeneous environments have higher species diversity, they are more resilient, and less variable. They are less susceptible to pest outbreaks, perhaps because there are more natural predators for potential pests and there are more patchways through which a population increase can dissipate. Heterogeneity is also important for speciation, because it allows geographic isolation of populations. It is the sheer scale of human operations that make them unsustainable.

Tree farms do not replace native forest. Monocultures may be technically and organizationally practical, but they are unstable and not robust. They have low diversity of associated species. They are susceptible to disease and parasite outbreaks. They are often based on exotic species that may grow fast initially but mine the soil for nutrients and moisture unsustainably. The rapid growth is possible only because of the free ecosystem service provided by the original forest: producing nutrient rich soils, retaining moisture, pest control, erosion control and flood control. When the original forest is gone, these precious resources are rapidly depleted.

Principles for habitat management

• maintain critical ecological processes

Among the critical ecological processes that need to be maintained are:

- hydrological feedback mechanisms
- gas exchange
- water recycling and purification
- nutrient cycling

For instance, forests play an important role in determining local local climate (by affecting albedo, moisture levels, and temperature), in water purification, erosion control, flood control, carbon dioxide removal, etc. People's livelihood often depends directly on forest, watersheds, wetlands or particular animals and plants therein, and *always* indirectly. "Our sense of the whole, that is its integrity, has to do with its ability to maintain its organization and to continue its process of self-organization. If a system is unable to maintain its organization, in the face of changing environmental conditions, then it has lost its integrity" (Kay 1993)

• conserve evolutionary processes

Species evolve over time — but it takes time, lots of time. Species change to better utilize the opportunities their environment provide, and to track changes in the environment. New species evolve from old species. To do that they must have old species to evolve from. Preserving evolutionary processes means preserving the raw material on which evolution acts. Evolution acts by selecting from a pool of genetic diversity. Each species has its own pool of genetic diversity to select from. The more species, the more genetic diversity overall. But not all species are equal. When a species has been reduced to a small number of individuals at some time in its past, its genetic diversity is limited to that present in those few individuals, and what little has had time to arise by mutation since then. EX: The cheetah has gone through repeated population bottle necks in the past as its range has been restricted. As a consequence, the cheetah has nearly no genetic diversity to allow individuals to survive changes in their environment. Furthermore, fecundity and juvenile survival are very low in cheetahs and they are susceptible to new diseases. The long term survival of the cheetah is therefore uncertain.

• preserve the natural patch structure and disturbance regime

Managers should strive to mimic natural patterns and processes. Reserves and other management units must be large enough that the natural patch structure can be reproduced at the landscape level.

• preserving communities vs. "hitchhikers"

One can argue about whether management efforts should focus on protecting individual species, or whole communities (or ecosystems). To protect individual species, one must protect their habitat and this involves preserving the integrity of the system. In some cases, we can focus on individual species and let the rest of the community be "hitchhikers". In any case, to manage successfully we need to:

- Obtain biological inventories
- Estimate population sizes for particularly vulnerable or important species
- Conduct population viability analyses
- Maintain adequate funding for protection and monitoring of the focal habitats
- Collect data on the changes, so that one can learn from the experiment and modify management practices in response to any surprises
- Publish the results

Recommendations for managers and policy makers

What you can do in any particular case or region depends on what other activities are ongoing in the region and what other pressures are being put on the region. Ecology is the study of species interactions and patterns in distribution and abundance of species. It is necessarily holistic in nature, and natural systems cannot be studied in isolation. Or rather, while natural systems can be studied in a reductionistic fashion, management of them must be holistic. In isolation, most projects may have a slight negative impact on natural habitats and biodiversity. They must, however, be seen in conjunction with all other human activities in the area. In concert their combined impact may be devastating even if each little project in itself has little impact. Furthermore, there is an insidious ratchet effect that occurs when "nobody remembers what the place used to be like". Short memory establishes a moving base-line for comparison. While the environment slowly deteriorates, every little new project has only a slight detrimental effect (though threshold effects may kick in when least expected). Here is another role for detailed biological inventories and status estimates for species in the area before any new projects are initiated — providing a record of early conditions, and periodic monitoring of changes. We also need to preserve virgin habitats as reference sites for scientific inquiry and comparison.

The considerations relevant to the management of a fishery will differ from those of managing a tropical forest, which will differ from relevant considerations to a project that will affect a river — detailed studies must be conducted in each case. Indeed, two rainforest sites will be sufficiently different that on site studies must be carried out, and of course the scope of such studies will be different for different kinds of projects. Simple answers are never adequate in complex systems, and complexity has to be dealt with explicitly.

We need to strengthen research and the protection of natural habitats while enhancing the dissemination of research findings and expounding the value of conservation. Effective reserve management is much easier when the local people benefit directly from the reserve and are aware of the many indirect ways in which the reserve contributes to their subsistence. A self-reliant local populace that benefit economically will take pride in "their" reserve and play an important role in protecting and preserving it.

Remember the human component of ecosystems. Human habitation can be compatible and even enhance regional biodiversity if on a small scale, with low intensity, not overly specialized, extraction of natural products, preferably on a temporary basis — abandoning the site and allowing nature to reclaim it. One of the quickest and easiest ways to reduce habitat degradation in many developing countries would be to distribute propane stoves/burners and sufficient supplies of gas free or nearly free of charge to rural communities that would otherwise rely on fuel wood consumption. Even better would be to stimulate a self-reliant local industry of distribution and maintenance of reliable solar panels or solar cookers. This would greatly reduce the rate of forest degradation while freeing up a lot of time for women in the countryside. Socioeconomic considerations relevant to natural habitats management options are discussed at length elsewhere (e.g. Wells and Brandon 1992).

Small scale experimentation should play a larger role in habitat management as well as in environmental impact assessments.

There is a great need for basic ecological knowledge in order to carry out environmental impact assessments. Much of this information is not presently available. Furthermore, much of ecologists' limited ability to make limited, specific predictions about the outcome of any perturbation comes not from theory, but from experience — similar cases where controlled or accidental/natural experiments have been conducted. Governments, large companies and organizations, especially development organizations, also carry out a lot of small and large scale projects that are essentially biological experiments. Detailed biological inventories and ecological descriptions of areas affected before and after project initiation, and continued monitoring by ecologists, would drastically augment the communal knowledge about ecological systems — both pure and applied. This benefit would be particularly acute in tropical environments, where our understanding of the ecology is particularly fragmented and limited. This database of accumulated experience from previous projects could quickly become a most powerful resource in environmental assessment and natural habitats management. The benefit to science would be substantial. The data and study summaries obtained through these endeavors should be published and made available to the public.

A world with islands of human development in a sea of natural habitat is much more robust than islands of natural habitat in a sea of human development.

We have come to the point where the best long term investment any country can make is to freeze development/encroachment in all of its remaining virgin habitat areas immediately. With continued expansion the physical limits must be faced sooner or later. Sooner is better than later: preservation now is cheaper, more effective, and more politically palatable while investments are still low; sooner maximizes available management options. Remaining pristine areas will contribute immeasurably to the wealth and quality of life in all countries in the future if preserved today. Development organizations, governments and international lending institutions like the World Bank, can play an important role in helping countries achieve such a freeze, and in optimizing use of already disturbed areas. Towards this end we should a) relocate harvesting from primary forest to secondary forest, b) aid in the relocation of poor farmers from marginal land to more valuable land that has already been disturbed for other purposes (cattle ranching, export production, etc.).

Ecologists must be consulted at every stage of the project, and monitoring must be continued after the project is otherwise completed. Detailed biological inventories should be conducted before any project is approved, and the ecological constraints must be identified in every project individually. When this information is available, geographic information systems (GIS) are often useful to identify areas of particular biological diversity and importance, and identify abiotic landscape features with particularly important functions in the local environment.

Concluding thoughts

There is no adequately developed theory of extinction. We do not know how much functional redundancy there is in natural communities. In that sense, ecology is not yet an exact predictive science. The complexity of the underlying biological and physical systems precludes a reductionist approach to management. When ecologists can predict, it is usually in a very narrowly defined question in a very specific setting, and it is usually because the experiment has already been done — they have seen a similar event happen earlier — not because their models have predictive power. Most of this experience is gathered in temperate countries in the developed world. The collective scientific experience in tropical systems is very limited. Development organizations, NGOs and international lending institutions could play an important role in funding and contracting for specific, small scale experiments to be conducted when specific knowledge is needed.

Large levels of natural variability mask the effects of overexploitation. Effective policies are possible under conditions of uncertainty, but they must take uncertainty into account. Stochastic effects must be incorporated in population models and in economic models involving the dynamics of natural populations (e.g. harvesting models, see Lande et al. 1994). We must consider a variety of plausible hypotheses about the world; consider a variety of possible strategies; favor actions that are robust to uncertainty; hedge; favor actions that are informative; probe and experiment; monitor results; update assessments and modify policy accordingly; and favor actions that are reversible (Ludwig et al. 1993).

Err on the side of caution. In natural habitats management, every gain is temporary while every loss is permanent. While the causes of biodiversity loss are clear, the consequences are not. We must abide by the precautionary principle in case the consequences are more dire than we can imagine today. Loss of biodiversity is irreversible, and there is no way we can correct our mistakes when a species is lost. Conservation biology is a crisis discipline, and sometimes we have to make decisions before all the information is in, and we often have to act before final proof of an effect is on the table. As the extinction crisis continues and we go into a biodiversity deficit, the margin of error is going to diminish. The burden of proof must be on the developer.

Every advance in conservation and management will be negated by continued human population growth. Impact = Population × Affluence ×Technology. This equation was proposed by Ehrlich and Holdren in 1974. It is perhaps better rewritten as Impact = Population × Consumption × Technological inefficiency. Technological inefficiency represents the environmental damage per unit of consumption. With the same technology, increased population or increased consumption has the same effect on environmental impact. In the last century world population has grown by about 2% annually, doubling about every 35 years, while consumption has grown at about twice that rate. The big increase in impact may come from increased consumption in highly populated areas (great potential for rapid increase in consumption in some countries, great overconsumption in others). The average energy consumption of a resident of the United States is about 200 fold higher than that of a resident of Ethiopia. The potential increase in consumption in developing countries is much greater than the potential population increase. Consumption must be reduced in many developed countries, population growth must be halted in developing countries and the United States, and developing countries must not aspire to the kind of consumption we have seen in the so-called developed countries. The prospect of one billion Chinese and one billion Indians exchanging their bicycle for an automobile is truely frightening.

A doubling of global human population size, with or without a potential 30 fold increase in consumption in some developing countries, will — at best — severely strain the life-support systems of planet Earth. Rapid loss of millions of species is probably inevitable under such a scenario. The consequences to humanity of such a loss are impossible to predict due to the many complex, nonlinear ways that components in ecological systems interact and the many complex interactions and feedback mechanisms between biotic and abiotic factors in the biosphere.

Innovative efforts at energy conservation should always be seriously considered before increased energy extraction projects are instigated. Humans eating high on the foodchain are a much greater burden than those eating low on the foodchain, due to the inefficient transfer of energy between trophic levels.

With continued human population growth, natural ecosystems may become untenable. The temptation to try and manage the global environment by our own power may become overwhelming as the opportunity costs of any undeveloped areas become politically unbearable. Such hubris demonstrates a lack of understanding of the complex feed-back mechanisms in nature. Ecological constraints compel us to reduce the scale of human operations. Perpetual growth is the creed of the cancer cell (Edward Abbey).

> *"If the earth must lose that great portion of its pleasantness which it owes to things that the unlimited increase of wealth and population would extirpate from it, for the mere purpose of enabling it to support a larger, but not a happier or a better population, I sincerely hope, for the sake of posterity, that they will be content to be stationary, long before necessity compels them to it".*
>
> — John Stuart Mill
>
> (1857)

Even slash and burn agriculture in tropical rainforests can be practiced sustainably if there are not too many people in too small an area, so that cleared areas can be abandoned and allowed to regenerate before it is used again. If sustainable use and sustainable development is possible, it is clearly only possible below a given population density of human beings at a given level of consumption. For a recent review of human population growth and global carrying capacity see Pulliam and Haddad (1994).

Time is critical. The global biodiversity crisis is in full force already, though the full brunt of its consequences will not be felt by humans for many years. Some repercussions are already being felt, in a limited way, by people who live directly in the beleaguered habitats of our ecosystems. The battle may be irretrievably lost in ten to twenty years. Education is important, but we cannot rely on education, as the next generation of opinion makers and policy makers will come too late. Education of present-day policy makers is a higher priority.

The costs of ignoring the ecological constraints are always delayed. Projects can have ecological side-effects the costs of which can outstrip any benefit from the project.

Present commitments to global conservation are clearly inadequate. Additional reserves are needed to improve representation of diverse biotas and to fill some of the large gaps between existing reserves. Better protection is needed for existing reserves, and more care must be taken to preserve biodiversity outside reserves. Aside from the economic costs of ignoring ecological constraint, either through the disruption of ecosystem services or the elimination of valuable products, humans have a moral responsibility not to destroy what are our only known living companions in the universe. The popularity of ecotourism, bird-watching, pets, wildlife films, gardening testify to the esthetic pleasure we derive from nature (and great economic activity derived therefrom). A reverence for nature is partially reflected in people's great willingness to pay for the protection of natural habitats even if they will never see them themselves. It is important for our spiritual life to have biological diversity around.

The developed world could easily cover the expenses of natural habitats and wildlife conservation in developing countries or supply the initial investments until such time as they can pay for themselves.

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Glossary

carrying capacity	A measure of the amount of renewable resources in the environment in units of the number of individual organisms these resources can support. In some usages, the equilibrium density of a logistic (sigmoidal) equation of population growth — the maximum population size that can be sustained by a given environment.
commensalism	An interaction where one organism (or species) beneficially affects another, but the latter has no effect on the former.
competition	An interaction where two organisms (or species) negatively affect each other, depressing their birth and/or growth rates and/or increasing their death rates.
endemic species endemism	Species with an exclusively local range (at a given spatial scale).
guild	A group of organisms in a given taxon that are ecologically similar, and play similar ecological role in the community — they have similar ecological niches.
heterozygosity	A measure of population genetic variation — the frequency of individuals with different varieties of a given gene in a chromosome pair.
keystone species	A species whose presence has a disproportionate effect on the community structure. For instance, a top predator that enable other species to coexist in the community, or a species that is a critical food resource to many other species.
metapopulation	A set of semi-isolated populations linked by potential dispersal, some times partially isolated in distinct habitat patches or remnants, possibly with dispersal corridors between them.
stochasticity	Randomness, of a process that is subject to random events, as opposed to being deterministic.
umbrella species	A species whose preservation or management indirectly serves to preserve many other species. For instance, if it requires such a large area to persist, that most other species in the community also can persist in that area.