S. Afr. J. Mar. Sci. **12**, 975 (1992).
44. J. F. Caddy and R. Mahon, *FAO Fish. Tech. Pap.* **347** (1995).
45. Saetersdal, *Rapp. P. V. Reun. Cons. Int. Explor. Mer.* **177**, 505 (1980); J. Caddy and J. Gulland, *Mar. Policy* 7, 267 (1983); V. S. Kennedy and L. L. Breisch, *J. Environ. Manage.* **16**, 153 (1983); A. A. Rosenberg , M. J. Fogarty, M. P. Sissenwine, J. R. Beddington, J. G. Shepherd, *Science* **262**, 828 (1993); B. Holmes, *ibid.* **264,** 1252 (1994); M. J. Fogarty and S. A. Murawski, *Ecol. Appl.,* in press.
46. C. J. Walters and P. H. Pearse, *Rev. Fish Biol. Fish.* **6**, 21 (1996).
47. M. P. Sissenwine and J. G. Shepherd, *Can. J. Fish. Aquat. Sci*. **44**, 913 (1987); P. Mace, *ibid*. **51**, 110 (1993); R. A. Meyers *et al*., *ICES J. Mar. Sci*. **51**, 191 (1994).
48. A. P. Dobson, A. D. Bradshaw, A. J. M. Baker, *Science* **277**, 515 (1997).
49. B. A. Menge, *Ecol. Monogr*. **65**, 21 (1995).
50. D. Tilman and J. A. Downing, *Nature* **367**, 363 (1994).
51. R. M. Peterman and M. J. Bradford, *Science* **235**, 354 (1987); R. M. Peterman, M. J. Bradford, N. C. H. Lo, R. D. Methot, *Can. J. Fish. Aquat. Sci.* **45**, 8 (1988).
52. E. Ostrom, *Governing the Commons: The Evolution of Institutions for Collective Action* (Cambridge Univ. Press, Cambridge, 1990).
53. B. J. McCay, *Ocean Coast. Manag*. **28**, 3 (1995); *Special Issue: Individual Transferable Quotas*, B. J. McCay, Ed., *Rev. Fish Biol. Fish.* **6** (1996).
54. E. Pinkerton, Ed., *Co-operative Management of Local Fisheries: New Directions for Improved Management and Community Development* (Univ. of British Columbia Press, Vancouver, Canada, 1989).
55. J. C. Castilla, *Ecol. Int.* **21**, 47 (1994); J. C. Castilla *et al*., *Can. J. Fish. Aquat. Sci.*, in press.
56. B. J. McCay, in *Limiting Access to Marine Fisheries: Keeping the Focus on Conservation*, K. L. Gimbel, Ed. (Center for Marine Conservation and World Wildlife Foundation, Washington, DC, 1994), pp. 380–390; S. Hanna, *ibid*., pp. 391–400.
57. S. M. Garcia, *Ocean Coast. Manag.* **22**, 99 (1994).
58. R. M. Peterman, *Can. J. Fish. Aquat. Sci.* **47**, 2 (1990).
59. C. Clark, *Ecol Appl.* **6**, 369 (1996).
60. A. D. MacCall, *Dynamic Geography of Marine Fish Populations* (Univ. of Washington Press, Seattle, WA, 1990).
61. C. H. Peterson, *Aust. J. Ecol.* **18**, 21 (1993).
62. M. E. Power *et al*., *Bioscience* **46**, 609 (1996).
63. We thank C. M. Dewees, M. E. Power, W. G. Pearcy, S. R. Carpenter, D. R. Strong, G. Rose, F. Micheli, P. Mundy, M. Orbach, and M. Fogarty for helpful comments. J.C.C. and C.H.P. acknowledge support by the Pew Charitable Trust. J.C.C. also thanks the Center for Marine Conservation, USA. L.W.B. acknowledges support by U.S. GLOBEC and Sea Grant.

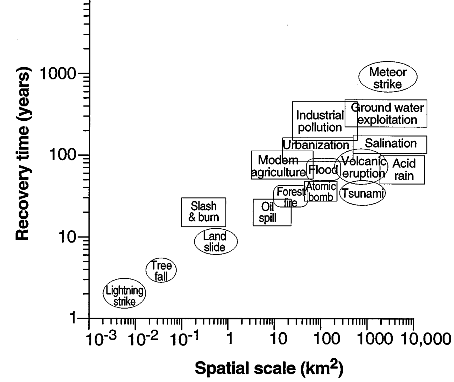

Fig. 1. The relation between the spatial scale of natural and anthropogenic disasters and their approximate expected time to recovery. Natural disasters are depicted in ellipses, and anthropogenic disasters are represented by rectangles. The data used to construct the figure were taken from a number of sources (*6, 13, 32*).

Hopes for the Future: Restoration Ecology and Conservation Biology

Andy P. Dobson, A. D. Bradshaw, A. J. M. Baker

Conversion of natural habitats into agricultural and industrial landscapes, and ultimately into degraded land, is the major impact of humans on the natural environment, posing a great threat to biodiversity. The emerging discipline of restoration ecology provides a powerful suite of tools for speeding the recovery of degraded lands. In doing so, restoration ecology provides a crucial complement to the establishment of nature reserves as a way of increasing land for the preservation of biodiversity. An integrated understanding of how human population growth and changes in agricultural practice interact with natural recovery processes and restoration ecology provides some hope for the future of the environment.

The impact of humans on the natural environment occurs at a variety of temporal and spatial scales. Industrial accidents, such as the *Exxon Valdez* oil spill or the meltdown at Chernobyl, often dominate the world's headlines and produce sudden dramatic ecological change over a large, but usually restricted, area of the landscape. Other changes—such as industrial pollution, deforestation, and conversion of natural habitats into agricultural and industrial land—occur chronically over large sections of each continent. All of these anthropogenic activities alter the habitat available for most other species and usually lead to a reduction in biodiversity.

Where catastrophic environmental changes occur, their major impact on biodiversity occurs instantaneously, although residual effects may last for several years. In contrast, the impacts of long-term habitat conversion may occur over a much longer time scale as individual species become threatened and eventually go extinct. Moreover, the disruptions in community structure and ecosystem function that occur as species are lost will exacerbate this accumulated extinction debt (*1*). Yet the scale and magnitude of these disturbances is often comparable with the "natural" disasters from which ecosystems usually recover (Fig. 1). In this review we describe how developments in restoration ecology and phytoremediation can be integrated with conservation biology to speed the recovery of natural ecosystems from local and more widespread anthropogenic changes. From the perspective of conservation biology, it is essential that restoration is undertaken before substantial losses of biodiversity have occurred. It is also crucial that the cleanup of industrial accidents have a minimum impact on biodiversity. In both cases, many of the more innovative and cost-effective approaches to solving these problems rely on harnessing natural ecosystem processes that are mediated by the different components of biodiversity.

Habitat Conversion and Loss of Biodiversity

Habitat conversion is the major threat to biodiversity. In particular, tropical forests (*2*), along with temperate forests, savannas, and coastal marshes, are being converted into land for agriculture, private homes, shopping malls, and cities. The length of time that the habitat remains viable for agricultural use is determined by the duration of soil productivity, or the rate of accumulation of weeds and other pest and pathogen species. Similarly, in areas of industrial activity, such as mining, use of an area commonly persists only until the mineral resource is exhausted; where there is manufacturing, use often comes to an end when the industry becomes outdated.

Throughout human history, habitat conversion has taken place at different rates and on different spatial scales (*3*). In

A. P. Dobson is in the Department of Ecology and Evolutionary Biology, Eno Hall, Princeton University, Princeton, NJ 08544–1003, USA. A. D. Bradshaw is in the School of Biological Sciences, University of Liverpool, Liverpool, L69 3BX, UK. A. J. M. Baker is in the Department of Animal and Plant Sciences, Alfred Denny Building, Sheffield University, Western Bank, Sheffield, S10 2TN, UK.

Europe, the Middle East, China, and Meso America, rates of habitat conversion were initially slow, and the deep alluvial soils underlying many of these areas have eroded slowly, permitting agriculture to persist for many centuries. In North America, habitat conversion has taken place more rapidly: Conversion has occurred in localized patches over the last 10,000 years, but the main changes have predominantly spread from east to west across the continent over the last 400 years (Fig. 2A). Strikingly, habitat conversion in the tropics has occurred primarily during the second half of the 20th century (Fig. 2B). This rapid rate of change has been caused by a number of economic and political forces driven by the large increases in the human population density in most tropical countries. In many places, widespread commercial logging of tropical forests has provided access into areas previously inaccessible to anyone other than the endemic groups who practiced low-level swidden agriculture. In the 1970s, the governments of Brazil and Indonesia provided tax incentives and other forms of political pressure that encouraged transmigration from areas of high human population density into areas that might be converted to agriculture (4). In developed countries, the same process can be driven by the common desire of new industry to establish on virgin "green-field" sites.

Habitat conversion from forests to agriculture and then to degraded land is the single biggest factor in the present biological diversity crisis (5). Data from various continents suggest that tropical forests (and temperate forests) are being destroyed at annual rates of between 1 and 4% of their current areas (2, 4, 6). A significant additional effect is that habitat conversion to agriculture is occurring on land that only retains its utility as agricultural land for 3 to 5 years; it is then abandoned when invasion by weeds or erosion of the topsoil reduces its agricultural viability (4, 7). These degraded areas will accumulate, because although natural colonization and succession will occur, the process can be slow and can produce considerably impoverished fauna and flora. Where widespread clearing has lead to the local extinction of previously common pioneer species and mid- and late-succession species, recovery occurs at a much slower pace. Models of habitat loss suggest that the process produces an "extinction debt," a pool of species that will eventually go extinct unless the habitat is repaired or restored (1). Although populations of some of these species may be maintained as captive populations in zoos and botanical gardens for eventual reintroduction, only a limited number of species are likely to be saved in this way (8). In contrast, restoration of the habitat before these extinctions occur may provide an important means of allowing a significant number of species to recover. This suggests that human efforts to aid habitat restoration will increasingly become a crucial aspect of the conservation of biodiversity.

Modeling habitat conversion. The basic dynamics of habitat conversion and recovery can be described by a simple mathematical model. This model examines the impact, at the landscape level, of habitat conversion driven by the agricultural needs produced by a growing human population. The structure of the model is similar to the compartmental susceptible-infectious-recovered (SIR) models used in epidemiology (9). In this case, the compartments

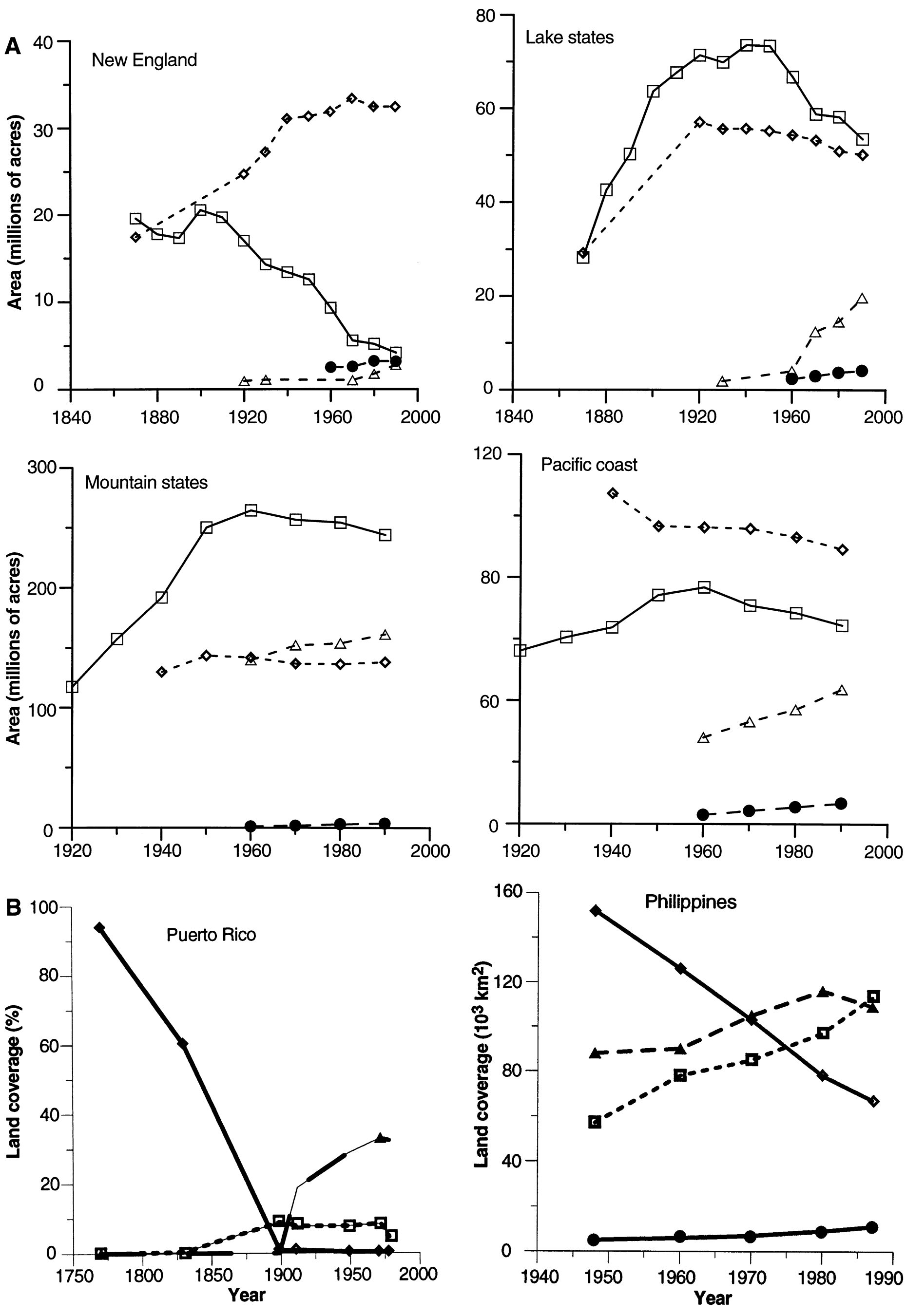

Fig. 2. (**A**) Changes in land use for four different regions of the United States, 1850 to 1990 [data from (49)]. The changes generally occurred from east (New England) to west (Pacific Coast). (**B**) Observed patterns of habitat conversion in the tropics: Puerto Rico (50) and the Philippines (4). Squares indicate farm area, diamonds are forest area, circles are urban areas, and triangles are miscellaneous (degraded) lands.

correspond to periods of time over which patches of converted natural habitat (such as tropical forest) can be used as agricultural (or industrial) land and the time that the resulting degraded land takes to recover to forest. The model also applies to areas used for industrial purposes that subsequently become obsolete, leading to the accumulation of derelict land, which then either recovers naturally or is reclaimed artificially.

The model considers the rate at which an original area of pristine forest habitat (of area F) is converted first to agricultural land (area A), which after a period of time $1/a$, becomes unused land (area U), which in turn recovers through natural succession or ecological restoration to become forest after a time interval $1/s$. Unused land may also be restored to agriculturally viable land after a time interval $1/b$. The basic parameters of the model can be readily estimated from current studies of tropical and temperate forests, and the framework is readily adaptable to other types of habitat. Rates of habitat conversion are assumed to be a simple function of the number of humans P using the land at any time. Initially this parameter is assumed to be constant; more detailed models can allow technological advances to lead to increases in the rates of habitat conversion. It is assumed that human population growth r occurs at a maximum rate of 4% and can be modeled as a simple logistic function with carrying capacity, given by the minimum amount of land h required to support an individual human. Technological and agricultural advances may also produce temporal changes in this parameter (*10*), but the initial assumption is that it remains constant. The basic form of the model consists of four coupled differential equations.

$$\frac{dF}{dt} = sU - dPF \tag{1}$$

$$\frac{dA}{dt} = dPF + bU - aA \tag{2}$$

$$\frac{dU}{dt} = aA - (b + s)U \tag{3}$$

$$\frac{dP}{dt} = rP\,\frac{A - hP}{A} \tag{4}$$

This framework assumes that we start with an initial area of forest F, which can be either the entire forest in a country or a patch of forest connected to other patches in a spatial array. The loss of biodiversity from the original habitat can be modeled in a number of different ways. In the simplest case, assume that the total number of species NS of any taxon living in the habitat of area A can be estimated using a simple power-law relation, $NS = cA^z$ (*11*) (c is a constant of proportionality, and Z is the power-law constant). A number of studies have shown that this relation provides a useful estimate of the proportion of species that will be found in a habitat as its total area declines (*12*).

The equations provide a framework in which to compare the impact on natural habitats of agricultural expansions, ecological restoration, improvements in agricultural efficiency, and human population growth. It is important to note that although the equilibrium dynamics are unaffected by the rate of growth of the human population, the transient dynamics are strongly dependent on the rate of human population increase: The more rapidly the human population increases, the more rapidly the forest is degraded and the landscape becomes dominated by unused land (Fig. 3A).

The equilibrium expressions for each of the model's variables (denoted by an asterisk) can provide simple insights into the factors that determine the proportion of each type of habitat that will be present once the system has reached a steady state.

$$A^* = hP^* \tag{5}$$

$$U^* = \frac{aA^*}{(s + b)} \tag{6}$$

$$F^* = \frac{ah}{d}\left(\frac{s}{s + b}\right) \tag{7}$$

The size of the human population at equilibrium depends on the initial total area F_0

$$P^* = \frac{\left(F_0 - \dfrac{ah}{d}\right)\left(\dfrac{s}{s + b}\right)}{h\left(\dfrac{a}{s + b} + 1\right)} \tag{8}$$

The equilibrium results illustrate the sensitivity of the resultant landscape to the rate processes, which determine the duration of time for which the land can be used for agriculture ($1/a$) and the length of time it takes to recover from degraded land to forest ($1/s$) (Fig. 3B). The most striking result of this analysis is that as the length of time for which land can be used for agriculture increases, the less forest remains in the final landscape. This situation corresponds fairly closely to Europe and the American prairies today. It would also apply to successful industrial areas, where one industry is succeeded by another and derelict land is reused immediately. In contrast, when land can only be used for agriculture for a short time and human population density is low, it is possible that significant amounts of forest remain, a situation that corresponds to swidden agriculture in many tropical forests up until the early 20th century. In all cases, increases in the land available to agriculture will result from reductions in the recovery time from previous exploitation. It is also important to notice that the amount of natural habitat remaining at equilibrium (F^*) decreases both with the efficiency with which humans convert natural habitat to agricultural land (d) and with the efficiency agricultural production ($1/h$). Moreover, further reductions in the natural habitat remaining at equilibrium are likely to occur if restoration produces new agricultural land, rather than "natural" habitats.

It is possible to build modifications into this basic framework. In many cases, tropical deforestation is not primarily the result of conversion for agriculture but is to open up logging roads for selective logging (*4, 6, 13*). This phenomenon can readily be included into the model with the addition of another equation. Similarly, the model can include more subtle details of the way in which human population growth responds to changes in resources (*14*). Alternatively,

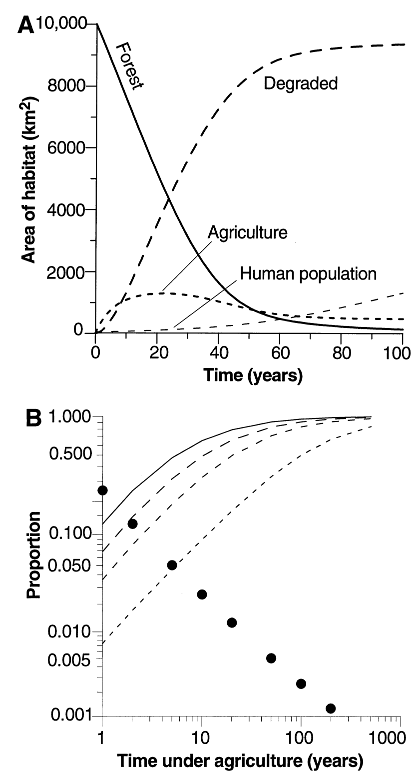

Fig. 3. (**A**) The transient dynamics of the model when an initial patch of 10,000 km^2 of forest are invaded by 50 people. Pristine forest declines and the area under agricultural land increases, as does unused and unusable land that is slowly recovering to forest. (**B**) The relation between the period of time for which land remains viable for agriculture and the proportion of habitat remaining in its pristine (or recovered) state (large dots). The contours illustrate the proportion of agricultural land in a landscape: They are drawn for a range of times that reflect different rates of recovery of degraded land back into forest (solid line, 5 years; long dashes, 10 years; intermediate dashes, 20 years; short dashes, 100 years).

additional expressions for resources such as water may be included; because resources such as water are vital to agricultural activity and human welfare and may require large areas of natural habitat to act as watersheds, the inclusion of these resources may lead to significant increases in the amount of land that remains as natural habitat.

Habitat conversion and the loss of biological diversity. All of this work presents a fairly pessimistic outlook for the future of the biological diversity that inhabits tropical and temperate forests. Although it seems likely that small patches of forest will remain, these patches are likely to be of the order of the size of the small patches of pristine forests remaining in Europe and the eastern United States. If the land can support agriculture for prolonged periods of time, the bulk of the landscape is dominated by agricultural land. In contrast, where fragile soils allow only short-term agriculture, the landscape becomes dominated by degraded land that is slowly recovering into forests. The same principles apply to land used for industrial areas.

This situation suggests two main approaches for the conservation of biodiversity. The simplest and most crucial is the setting aside of protected areas of land as parks and nature reserves. It is crucial that, within these, a full range and sufficient amount of "original" ecosystem is retained because they will provide the natural colonists for the regeneration of degraded patches. Mapping and geographical information systems will provide important methods for identifying key areas of habitat for endangered species (*15*).

The second main approach is the restoration of degraded agricultural and industrial land, to reduce the pressure for further natural habitat conversion by providing lands that can be used for agricultural or recreational activities, and even to provide new land for nature reserves. In a world where development should be curtailed yet all agricultural and industrial development cannot be stopped, there is intense psychological and practical importance to growing new, or restored, ecosystems. Indeed, restoration can now be considered a critical element in managing the world's environment. It provides a powerful way of reducing the length of time for which habitat remains in the degraded and unused category of the simple model described above.

Lessons from Primary Succession

In the current climate of gloom over the future of our environment, people tend to think that all environmental damage is irreversible. It is not. The functioning ecosystems in every part of Earth's surface, including such inhospitable locations as moraines left by retreating glaciers (*16*) and the dunes formed by the accretion of lake shore sand (*17*), originated in the natural processes of primary succession (*18*). Primary succession is ecosystem development in situations where no previously developed soil exists. The processes involved fall into two groups, biological and physical (Table 1). Although the primary characteristics of habitats are physicochemical, the biological processes, particularly the processes of nutrient accumulation, are more important for the development of a habitat that can support a properly functioning ecosystem. This dependence on biology is especially true for nitrogen because in soils it is stored only in organic matter, from which it is released by slow decomposition. In temperate regions, where decomposition rates are 10% per year or less, the soil must accumulate at least 1000 kg of N per hectare to provide for the annual needs of an ecosystem (about 100 kg of N per hectare). Because the initial degraded material is likely to have very little nitrogen, accumulation is frequently the limiting factor controlling ecosystem development (*19*).

In primary successions, community development accompanies the development of the habitat. The establishment of different species can be determined by chance, the state of the habitat, and interactions between new species and those already present. These processes are recognized in the alternative models for the mechanism of succession of tolerance, facilitation, and inhibition (*20*). In situations in which the environment is degraded by human activity, the processes of primary succession bring about ecosystem development in the same manner; examples include hard-rock quarries (*21*), ironstone banks (*22*), and kaolin mining wastes (*23*). The early stages of succession, characterized by the poverty and openness of the ecosystem, help generate ecosystems rich in species sensitive to competition that cannot find living space in more developed ecosystems (*24*). The processes of secondary succession (ecosystem development in situations where the original soil remains) also have a bearing on what may be achieved. However, secondary succession represents, ecologically, a simpler problem, most of which is included in primary succession.

Table 1. The time scales for biological and physical processes involved in the development of ecosystems on a newly produced bare area.

Biological processes		Physical processes	
Time scale (years)	Process	Time scale (years)	Process
1–50	Immigration of appropriate plant species	1–1000	Accumulation of fine material by rock weathering or physical deposition
1–50	Establishment of appropriate plant species		
1–10	Accumulation of fine materials captured by plants	1–1000	Decomposition of soil minerals by weathering
1–100	Accumulation of nutrients by plants from soil minerals	1–100	Improvements of soil available water capacity
1–100	Accumulation of N by biological fixation and from atmospheric inputs	1–1000	Release of mineral nutrients from soil minerals
1–20	Immigration of soil flora and fauna supported by accumulating organic matter		
1–20	Changes in soil-structure and organic-matter turnover due to plant, soil microorganism, and animal activities		
1–20	Improvements in soil water-holding capacity due to changes in soil structure	10–10000	Leaching of mobile materials from surface to lower layers
10–1000	Reduction in toxicities due to accumulation of organic matter	100–10000	Formation of distinctive horizons in the soil profile

Ecological Restoration

The problem with leaving restoration to natural processes is that they take time, measured in decades or centuries (Table 1); redevelopment of advanced communities may take a millennium or more. However, this long time scale is due to specific problems that, once identified, can be overcome by artificial interventions, which are most successful if they use or mimic natural processes. This process of identification and intervention is the essence of ecological restoration.

The substrate. The soil usually provides the major problems, but for each problem, there are immediate and long-term treatments (Table 2). For example, nitrogen deficiency can be overcome in the short term by the application of artificial or organic fertilizers, and in the long term by the introduction of nitrogen-fixing plant species. A range of herbaceous and woody species, which can accumulate over 100 kg N ha^{-1} $year^{-1}$, can be used to raise the nitrogen capital of the soil: For instance, herbaceous legumes such as *Trifolium* and *Lespedeza* have been used temporarily in the restoration of pasture land on coal wastes in the United Kingdom and Australia, and tree species such as *Casuarina* and *Acacia* are an integral part of the final ecosystem in the restoration of forests on metal and coal mine wastes in India. The use of nitrogen-fixing species requires good knowledge of their biology, both their soil preferences and their interactions with other species. Although many of the structural characteristics of soils take a long time to restore, the restoration of their biological properties can usually be brought about swiftly, so that proper ecosystem function can be achieved within 10 years.

These treatments can often be obviated if the original soil can be removed before disturbance and replaced afterward, as is now required for surface mining in most developed countries. But a considerable backlog of sites where this has not been done exists throughout the world, and many situations occur where it is still not required. In 1974 in the United States, the total area of degraded land resulting from surface mining alone was over 1,784,000 ha; in Britain, the total amount of officially recognized derelict land was over 43,000 ha. Recent surveys suggest little change because the restoration level has been matched by the accumulation of additional dereliction. Similarly, data from the Food and Agriculture Organization (FAO) on the conversion of forests into agricultural land in the tropics show that the loss of forests is more closely matched by increases in degraded land than by increases in agricultural land (*25*).

The community. Once soil characteristics have been restored, it is not difficult to restore a full suite of plant species to form the required vegetation. The common approach has been to choose (i) species important for restoring ecosystem function, together with (ii) species that are to be the main components of the final ecosystem, leaving (iii) the many plant and animal species that should make up the final biodiversity of the ecosystem to recolonize by their own efforts. It is now realized, from studies of chemical waste heaps (*26*) and the area covered by the eruption of Mount St. Helens (*27*), that the recolonization of the final biodiversity is likely to be slow and unreliable, because so many of the desired species are no longer available in the vicinity and migration over long distances can be limited.

There is considerable interest in devising means for enhancing natural immigration that results from the natural processes of seed dispersal by encouraging the movement of seed carriers, especially birds (*28*). Where this approach is not possible, artificial reintroduction must be used. More information is needed about the establishment characteristics and requirements of individual wild species, as is illustrated by current work on European heath communities: The establishment of heath species that require low amounts of nutrients and lots of light, such as *Calluna*, can be aided by the addition of fertilizer and the presence of a grass species that act as a "nurse" (*29*). Much has been hypothesized about assembly rules for communities; ecological restoration provides the opportunity to test these ideas. It appears that, so long as the environmental requirements for the establishment of the individual species can be met (and this may not be easy), species can be introduced together rather than sequentially. This method will not, however, apply in more highly structured communities—such as forests (*30*), especially high-diversity tropical forests (*31*)—where the age-determined elements of vegetation structure cannot be put back immediately. The current challenge of ecological restoration is to steer development so that all of the subtleties of structure and function recover, allowing the full range of species to find their niches (*32*). Nevertheless, there is always the possibility that the whole process may go in an undesired direction (*31, 33*). Species that arrive first by chance may persist and dominate the ecosystem for many decades, especially if they establish in large numbers. Manipulation of the initial composition of species may therefore be necessary.

Another gap in current knowledge is in determining how many of the component species of the final ecosystem can be left to enter the community on their own. Mobile species such as birds can certainly do this, provided that the developing ecosystem is suitably structured, as has been shown in gravel pit restoration (*34*). Fish and water plants usually cannot colonize unless the pits are connected to a river system, but they can be added as individuals or in soil or dredged mud. Many woodland species are immobile (*35*), so they must be added as seed or plants. For artificially introduced species, it is important to use individuals from the locality, which are well adapted to the environment. Evolutionary adaptation can take place specifically in relation to the conditions occurring in degraded habitats (*36*), suggesting that material from the degraded habitat itself is not necessarily most suitable for the final restored ecosystem. However, such adapted individuals will be valuable in the initial, degraded condition, and there is no reason such material will not adapt to subsequent improvements in the environment.

Phytoremediation. The most recalcitrant problem in restoration is the decontamination of soils polluted with heavy metals and certain organic compounds. Techniques in current use for metals are based on physicochemical extraction, such as acid leaching and electro-osmosis, or on in situ im-

Table 2. Short-term and long-term approaches to soil problems in ecological restoration.

Category	Problem	Immediate treatment	Long-term treatment
		Physical	
Texture	Coarse	Organic matter or fines	Vegetation
	Fine	Organic matter	Vegetation
Structure	Compact	Rip or scarify	Vegetation
	Loose	Compact	Vegetation
Stability	Unstable	Stabilizer or nurse	Regrade or vegetation
Moisture	Wet	Drain	Drain
	Dry	Irrigate or mulch	Tolerant vegetation
		Nutrition	
Macronutrients	Nitrogen	Fertilizer	N-fixing species
	Others	Fertilizer and lime	Fertilizer and lime
Micronutrients	Deficient	Fertilizer	
Toxicity	Low	Lime	Lime or tolerant species
pH	High	Pyritic waste or organic matter	Weathering
Heavy metals	High	Organic matter or tolerant plants	Inert covering or bioremediation
Organic compounds	High	Inert covering	Microbial breakdown
Salinity	High	Weathering or irrigate	Weathering or tolerant species

mobilization, for example, by vitrification, a thermal process in which metals are fused with the silica fraction of the soil to form an inert glass (*37*). These methods require specialized equipment and trained operators; they are therefore costly and only appropriate for the decontamination of small areas where pressure of land use or development potential merits the outlay. Furthermore, they remove all biological activity from the treated medium and adversely affect its physical structure and suitability for plant growth during revegetation.

In the last few years, there has been much interest in the potential offered by plant uptake of heavy metals as a means of soil decontamination (*38, 39*). The principle of phytoextraction (one form of phytoremediation) is simple and elegant in concept: The substrate is "cropped" for metals, which are progressively and selectively removed, leaving it in all other ways unaffected. The biomass is harvested, removed, and disposed of as hazardous waste or is incinerated at low temperature, allowing the recovery of the metals concentrated in the ash.

Some plants endemic to metalliferous soils are capable of accumulating exceptionally high concentrations of potentially phytotoxic metals such as Zn, Ni, Cd, Pb, Cu, and Co in their harvestable biomass. For these metals, some 400 hyperaccumulators have now been identified (*40*). Concentrations of metals can reach several percent in the above-ground dry biomass of these plants. In Europe, a large proportion of hyperaccumulators are members of the Brassicaceae (a family that includes many important crops): Included are species of the genus *Alyssum* found on serpentine (naturally Ni- and Cr-rich) soils in southern Europe, which can accumulate concentrations of Ni in excess of 2% on a dry-weight basis, and some *Thlaspi* species from calamine (naturally Zn-, Cd-, and Pb-rich) soils, which can accumulate Zn to more than 5%, Cd to 0.2%, and Pb to 1%. Hyperaccumulators of Zn, Ni, Cu, and Co have also been discovered in the metallophyte floras of the tropics and subtropics. They include representatives of many families and range in growth form from annual herbs to shrubs and trees. Baker *et al.* (*41*) used a range of Zn- and Ni-hyperaccumulator plants grown under intensive agronomic conditions to remove metals from agricultural soils contaminated in the rhizosphere (soil reachable by roots) through historical application of industrially contaminated sewage sludges. Uptake of Zn by the hyperaccumulator *Thlaspi caerulescens* was 30 kg ha^{-1}; subsequent provenance and agronomic trials elsewhere have pushed this value to well over 100 kg ha^{-1} and up to 2 kg ha^{-1} for Cd (*39*). This approach to phytoextraction is still under development in both the United States (U.S. Department of Agriculture's Agricultural Research Service, Beltsville, Maryland) and the United Kingdom (Institute of Arable Crop Research, Rothamsted). A commercial incentive to this development is that it has been estimated that the harvesting of 1 ha of *Thlaspi* yields 20 tons of biomass, which could contain over $1000 in recoverable metals.

The difficulties of using hyperaccumulator plants for wide-scale soil decontamination center on their relatively low biomass and slow rate of growth. Faster growing selection lines of annual *Brassica* crops such as Indian mustard (*B. juncea*) have been used for Pb phytoextraction (*42*). The lower concentration of metal in the *Brassica* shoots (compared to that in Pb hyperaccumulators) is more than compensated for by the greater biomass achievable and the possibility of growing multiple crops within a season.

Phytoextraction, either by exploitation of the unique physiological properties of hyperaccumulator plants or by means of high-biomass accumulator crops such as *B. juncea*, provides an attractive option for soil cleanup if the time scale is acceptable and the contamination is within the rhizosphere. Existing phytoextraction crops could also be improved through the use of conventional breeding techniques and genetic engineering approaches on high-biomass host plants. However, deep-seated contamination cannot be accessed by the roots; in these circumstances, plowing may be required. Bioavailability is also a problem, as metallic contaminants are usually present in insoluble and unavailable forms. The use of chemical amendments, such as chelating agents, to increase bioavailability in the rhizosphere has proven effective for Pb phytoextraction (*43*). There is considerable scope for enhancing metal bioavailability locally within the rhizosphere while protecting against leaching and ground-water contamination. Phytotech (Monmouth Junction, New Jersey) successfully used Pb phytoextraction at two brownfield (industrially contaminated) sites in New Jersey, cleaning most of the contaminated areas to state industrial standards (1000 mg kg^{-1} Pb) within one summer of multiple cropping with *B. juncea* (*44*). Phytoextraction also offers great possibilities for the decontamination of radionuclides such as ^{137}Cs and ^{90}Sr from contaminated soils and effluents and for the removal of excess Na, Se, and B from saline soils. Phytovolatilization (the use of plants to extract inorganic contaminants, which are then dispersed into the atmosphere by volatilization from aerial parts) of Se and Hg also provides considerable scope for commercial development (*44*).

A further variant of phytoremediation under development is phytostabilization, the use of plants to immobilize or stabilize metal contaminants in the soil (*38*). Gary Pierzynski of Kansas State University and Jerry Schnoor of the University of Iowa have used plants successfully to stabilize soils and decrease the movement of metals to ground water at a smelter Superfund site in Dearing, Kansas. Nothing has grown on the waste piles since the site was abandoned in 1919; concentrations as high as 20,000 mg kg^{-1} Pb and 200,000 mg kg^{-1} Zn made it impossible for even weeds to invade the site. The researchers planted 3100 hybrid poplar trees on two acres at the site with soil amendments. Survival has exceeded expectations, and the site is now revegetated. More importantly, the primary risk to humans in the vicinity, that of windblown dust, has been reduced.

Bioremediation technology for organic compounds has been developing faster than that for inorganics, so it is tempting to believe that for every type of organic contaminant a suitable microbial organism or consortium can be found with the capacity to degrade the contaminant in situ, ultimately into CO_2 and water. However, the major leap from in vitro demonstration to successful field decontamination has proved too great in many promising initiatives, but commercial bioremediation systems are now available for many of the more environmentally hazardous organic contaminants. Phytoremediation of organic contaminants is also proving possible either directly through plant uptake or by degradation or stabilization in the rhizosphere (*45*). In an attempt to obtain a better understanding of what occurs when plants are moved from the bench to the field, researchers at the University of Washington constructed a series of field test plots to study the interactions between a variety of trees and contaminated ground-water streams. This pilot scale study, using a series of artificial aquifers, allows them to compare accumulation, metabolism, and transpiration to a known level of exposure to trichloroethylene or carbon tetrachloride. This type of data may be crucial to the acceptance of this technology by more conservative remediation personnel. On the basis of conclusions drawn from laboratory data and results from the pilot site, the University of Washington group, in conjunction with the Oregon Department of Environmental Quality, are attempting to remediate an aquifer that was contaminated with 1,1,1-trichloroethane about 10 years ago. This site has been proposed for a detailed study of the efficiency of poplar trees in the remediation of a contaminated aquifer.

Outlook

Although human habitat conversion has generally been detrimental to most other species, restoration ecology is beginning to provide opportunities to reverse the trend and to create new habitats for biodiversity. Primary succession provides good evidence of the power of natural processes in recreating ecosystems without aid. When coupled with interventions aimed at treating any serious long-term problems that may occur, rapid improvements can be brought about. There are many examples of successful restoration (*46*): A single outstanding, current case is the restoration of the 10,000 ha of barren land around the nickel smelters at Sudbury, Ontario (*47*). With biologically based technologies such as phytoremediation, it will be possible to treat the most serious types of environmental damage in ways that not only restore a functional ecosystem but also recover resources that are valuable to industry. It is not yet clear the degree to which efforts should be aimed at true restoration (of what was there previously) as opposed to producing something new (replacing what was there originally), either modeled on other ecosystems or totally new artificial constructs. They are each possible alternatives (Fig. 4). To retain the world's biodiversity with the use of such creative conservation techniques can be effective and is welcomed by many conservationists. Whereas the principal aim of conservation biology will be to protect current nature reserves and national parks, while identifying and protecting unprotected areas that are also naturally rich in biodiversity (*15*), there is also a need for restoration to become a standard part of the conservation biologist's armory.

Although it is obvious that wherever possible environmental damage should not be allowed to occur in the first place, human development and population growth mean that damage is inevitable. The demands on land use are such that large areas of land will continue to be converted into agricultural and industrial areas. Increasingly, these will be "marginal" lands that will only be viable for agriculture for a short period of time. Ironically, the poorer soils of these areas may support a higher level of biodiversity than the areas with deep rich soils that have already been occupied preferentially (*48*). Rapidly restoring natural ecosystems that have only been transiently used for agriculture provides an important opportunity to ensure that development becomes sustainable. Most attempts at sustainable use of natural resources have focused at the population level, but we also need to consider the use of natural resources at the landscape level. Here the key to successful restoration will still rest on there being a potential pool of colonists that recolonize restored land. The only way to ensure this resource is to rigorously protect biodiversity in nature reserves and other natural habitats.

Ecological restoration will continue to provide important insights into the way that ecological communities are assembled and ecosystems function. There is a direct analogy with engineering: It is a relatively straightforward exercise to take apart an ecosystem or an automobile engine, yet quantifying the relative number of parts in an automobile engine (or an ecosystem) tells us little about how it functions. In contrast, reassembling the engine (or the ecosystem) will reveal a deeper level of understanding of how each of its components functions.

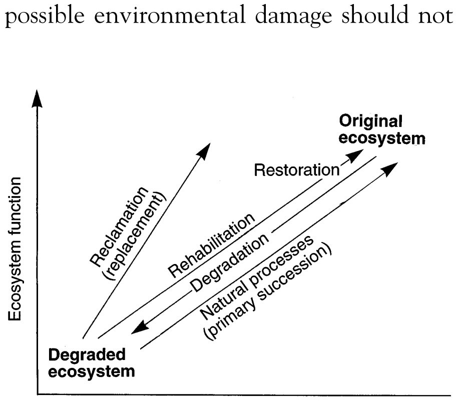

Fig. 4. Relation between ecosystem structure (which would include species diversity and complexity) and ecosystem function (for example, biomass, nutrient content, and cycling), illustrating changes that occur as a degraded ecosystem recovers toward its original state (*51*).

REFERENCES

1. D. Tilman, R. M. May, C. L. Lehman, M. A. Nowak, *Nature* **371**, 65 (1994).
2. W. V. Reid, in *Tropical Deforestation and Species Extinction*, T. C. Whitmore and J. A. Sayer, Eds. (Chapman & Hall, London, 1992), pp. 55–73; J. A. Sayer and T. C. Whitmore, *Biol. Conserv.* **55**, 199 (1991); T. C. Whitmore and J. A. Sayer, in *Tropical Deforestation and Species Extinction*, T. C. Whitmore and J. A. Sayer, Eds. (Chapman & Hall, London, 1992), pp. 1–14.
3. W. B. Meyer and B. L. Turner II, *Annu. Rev. Ecol. Syst.* **23**, 39 (1992); A. Goudie, *The Human Impact on the Natural Environment* (MIT Press, Cambridge, MA, 1990).
4. D. L. Skole, W. H. Chomentowski, W. A. Salas, A. D. Nobre, *Bioscience* **44**, 314 (1994); D. M. Kummer and B. L. Turner II, *ibid.*, p. 323.
5. W. V. Reid and K. R. Miller, *Keeping Options Alive: The Scientific Basis for Conserving Biodiversity* (World Resources Institute, Washington, DC, 1989); A. A. Burbridge and N. L. McKenzie, *Biol. Conserv.* **50**, 143 (1989); H. Koopowitz and H. Kaye, *Plant Extinction: A Global Crisis* (Christopher Helm, London, 1983); R. M. May, J. H. Lawton, N. E. Stork, in *Extinction Rates*, J. H. Lawton and R. M. May, Eds. (Oxford Univ. Press, Oxford, 1995), pp. 1–24; T. D. Sisk, A. E. Launer, K. R. Switky, P. R. Ehrlich, *Bioscience* **44**, 592 (1994); A. T. Durning, *Worldwatch Pap.* **117**, 1 (1993); S. L. Pimm, G. J. Russell, J. L. Gittleman, T. M. Brooks, *Science* **269**, 347 (1995); R. T. Watson *et al.*, *Global Biodiversity Assessment: Summary for Policy-Makers* (Cambridge Univ. Press, Cambridge, 1995).
6. D. Skole and C. Tucker, *Science* **260**, 1905 (1993); R. F. W. Barnes, *Afr. J. Ecol.* **28**, 161 (1990).
7. C. Uhl and C. F. Jordan, *Ecology* **65**, 1476 (1984); C. Uhl and P. G. Murphy, *Trop. Ecol.* **22**, 219 (1981); C. Uhl, in *Biodiversity*, E. O. Wilson, Ed. (National Academy Press, Washington, DC, 1988), pp. 326–332.
8. W. G. Conway, *Int. Zoo Yearb.* **24/25**, 210 (1986); T. J. Foose, in *The Last Extinction*, L. Kaufman and K. Mallory, Eds. (MIT Press, Cambridge, MA, 1993), pp. 149–178; J. H. W. Gipps, *Beyond Captive Breeding: Re-introducing Endangered Mammals of the World* (Oxford Univ. Press, Oxford, 1991); A. M. Lyles and R. M. May, *Nature* **326**, 245 (1987); B. Griffith, J. M. Scott, J. W. Carpenter, C. Reed, *Science* **245**, 477 (1989).
9. R. M. Anderson and R. M. May, *Infectious Diseases of Humans: Dynamics and Control* (Oxford Univ. Press, Oxford, 1991); R. V. O'Neill, R. H. Gardner, M. G. Turner, W. H. Romme, *Landscape Ecol.* **7**, 19 (1992); P. Faeth, C. Cort, R. Livernash, *Evaluating the Carbon Sequestration Benefits of Forestry Projects in Developing Countries* (World Resources Institute, Washington, DC, 1994).
10. M. L. Primack, *J. Econ. Hist.* **22**, 484 (1962); D. R. Headrick, in *The Earth as Transformed by Human Action*, B. L. Turner II *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 1990), pp. 55–67.
11. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, NJ, 1967); W. D. Newmark, *Biol. J. Linn. Soc.* **28**, 83 (1986); H. A. Gleason, *Ecology* **3**, 158 (1922); O. Arrhenius, *J. Ecol.* **9**, 95 (1921); D. Simberloff, *Tropical Deforestation and Species Extinction*, T. C. Whitmore and J. A. Sayer, Eds. (Chapman & Hall, London, 1992), pp. 75–90.
12. Studies of the extinction of woodland birds in the eastern United States indicate that this approach provides accurate estimates of the observed extinction rate [see S. L. Pimm and R. A. Askins, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 9343 (1995)]. A recent review of habitat loss and fragmentation [H. Andren, *Oikos* **71**, 355 (1995)] illustrates that percolation theory provides important insights into the fragmentation process that is concomitant to habitat loss.
13. D. Pimentel *et al.*, *Oikos* **46**, 404 (1986); L. E. Sponsel, T. N. Headland, R. C. Bailey, *Tropical Deforestation: The Human Dimension* (Columbia Univ. Press, New York, 1996).
14. J. P. Holdren and P. R. Ehrlich, *Am. Sci.* **62**, 282 (1974); J. E. Cohen, *Science* **269**, 341 (1995); P. M. Vitousek, P. R. Ehrlich, A. H. Ehrlich, P. M. Matson, *Bioscience* **36**, 368 (1986); G. C. Daily and P. R. Ehrlich, *ibid.* **42**, 761 (1992).
15. R. L. Pressey, C. J. Humphries, C. R. Margules, R. I. Vane-Wright, P. H. Williams, *Trends Ecol. Evol.* **8**, 124 (1993); J. M. Scott, B. Csuti, J. D. Jacobi, J. E. Estes, *Bioscience* **37**, 782 (1987); J. M. Scott *et al.*, *Wildl. Monogr.* **123**, 1 (1993); A. P. Dobson, J. P. Rodriguez, W. M. Roberts, D. S. Wilcove, *Science* **275**, 550 (1997).
16. R. L. Crocker and J. Major, *J. Ecol.* **43**, 427 (1955).
17. J. S. Olsen, *Bot. Gaz.* **199**, 125 (1958).
18. J. Miles and D. W. H. Walton, Eds., *Primary Succession on Land* (Blackwell, Oxford, 1993).
19. R. H. Marrs and A. D. Bradshaw, in *ibid.*, pp. 221–235; A. D. Bradshaw, *J. Ecol.* **20**, 151 (1938).
20. J. H. Connell and R. D. Slatyer, *Am. Nat.* **111**, 1119 (1977).
21. B. N. K. Davis, *Biol. Conserv.* **10**, 249 (1976).
22. G. A. Leisman, *Ecol. Monogr.* **27**, 221 (1957).
23. W. S. Dancer, J. F. Handley, A. D. Bradshaw, *Plant Soil* **48**, 153 (1977).
24. D. Ratcliffe, *Proc. R. Soc. London Ser. B* **339**, 355 (1974).
25. R. A. Houghton [*Bioscience* **44**, 305 (1994)] quotes FAO data for the period 1980 to 1985, which suggest that in the tropical regions of America, Africa, and Asia, forests are being lost at rates of 5.0, 2.8,

and 2.1 million hectares per year, respectively. Although agricultural lands are increasing at 3.3, 0.3, and 0.9 million hectares per year, degraded lands are increasing at rates of 1.7, 2.6, and 1.3 million hectares per year.
26. H. J. Ash, R. P. Gemmell, A. D. Bradshaw, *J. Appl. Ecol.* **31**, 74 (1994).
27. J. F. Franklin, J. A. MacMahon, F. J. Swanson, J. R. Sedell, *Natl. Geogr. Res.* **1**, 198 (1985); J. F. Franklin, P. M. Frenzen, F. J. Swanson, in *Rehabilitating Damaged Ecosystems*, J. Cairns Jr., Ed. (CRC Press, Boca Raton, FL, 1995), pp. 288–332.
28. G. R. Robinson, S. N. Handel, *Conserv. Biol.* **7**, 271 (1993).
29. Environmental Advisory Unit, *Heathland Restoration: A Handbook of Techniques* (British Gas, Southampton, UK, 1988).
30. W. C. Ashby, in *Restoration Ecology*, W. R. Jordan, M. E. Gilpin, J. D. Aber, Eds. (Cambridge Univ. Press, Cambridge, 1987), pp. 89–97.
31. D. H. Janzen, *Conservation Biology: The Science of Scarcity and Diversity*, M. E. Soule, Ed. (Sinauer, Northampton, MA, 1986), pp. 286–303; D. H. Janzen, *Science* **239**, 243 (1988); D. H. Janzen, *Trends Ecol. Evol.* **9**, 365 (1994).
32. W. R. Jordan, M. E. Gilpin, J. D. Aber, *Restoration Ecology* (Cambridge Univ. Press, Cambridge, 1987).
33. H.-K. Luh, S. L. Pimm, *J. Anim. Ecol.* **62**, 749 (1993).
34. J. Andrews, D. Kinsman, *Gravel Pit Restoration for Wildlife* (Royal Society for Protection of Birds, Sandy Beds, UK, 1990).
35. G. F. Peterken. *Biol. Conserv.* **6**, 239 (1974).
36. T. McNeilly, in *Restoration Ecology*, W. R. Jordan, M. E. Gilpin, J. D. Aber, Eds. (Cambridge Univ. Press, Cambridge, 1987), pp. 271–283.
37. U.S. Army Toxic and Hazardous Materials Agency, *Interim Tech. Rep. AMXTH-TE-CR-86101* (1987).
38. D. E. Salt *et al.*, *Biotechnology* **13**, 468 (1995); S. D. Cunningham and D. W. Ow, *Plant Physiol.* **110**, 715 (1996); D. Comis, *J. Soil Water Conserv.* **51**, 184 (1996).
39. R. L. Chaney *et al.*, *Curr. Opin. Biotechnol.* **8**, 279 (1997).
40. A. J. M. Baker and R. R. Brooks, *Biorecovery* **1**, 81 (1989); R. D. Reeves, A. J. M. Baker, R. R. Brooks, *Min. Environ. Manage.* **3**, 4 (September 1995).
41. A. J. M. Baker, S. P. McGrath, C. M. D. Sidoli, R. D. Reeves, *Resour. Conserv. Recycling* **11**, 41 (1994).
42. P. B. A. N. Kumar, V. Dushenkov, H. Motto, I. Raskin, *Environ. Sci. Technol.* **29**, 1232 (1995).
43. M. J. Blaylock *et al.*, *ibid.* **31**, 860 (1997).
44. M. E. Watanabe, *ibid.*, p. 182A.
45. S. D. Cunningham, T. A. Anderson, A. P. Schwab, F. C. Hsu, *Adv. Agron.* **56**, 55 (1996).
46. A. D. Bradshaw and M. J. Chadwick, *The Restoration of Land* (Univ. of California Press, Berkeley, CA, 1980); M. K. Wali, Ed., *Ecosystem Rehabilitation*, (SPB Academic, The Hague, 1992); J. M. Gunn, *Restoration and Recovery of an Industrial Region* (Springer, New York, 1995).
47. K. Winterhalder, *Environ. Rev.* **4**, 185 (1996).
48. M. Huston, *Science* **262**, 1676 (1993).
49. U.S. Bureau of the Census, *Statistical Abstract of the United States* (1952); *ibid.* (1962); *ibid.* (1972); *ibid.* (1982); *ibid.* (1990); *ibid.* (1993).
50. A. R. Barash, *Biol. Conserv.* **39**, 97 (1987).
51. A. D. Bradshaw, *Restoration Ecology and Sustainable Development*, K. Urbanska and N. R. Webb, Eds. (Cambridge Univ. Press, Cambridge, 1997).
52. A.P.D. would like to thank G. DeLeo, A. M. Lyles, S. J. Ryan, J. P. Rodriguez, and D. Wilcove for comments on the manuscript and G. Dorner for extracting the data on habitat conversion in the United States. A.P.D.'s work is supported by a grant from the Charles Stewart Mott Foundation to the Environmental Defense Fund.

Forests as Human-Dominated Ecosystems

Ian R. Noble and Rodolfo Dirzo

Forests are human-dominated ecosystems. Many of the seemingly lightly managed or unmanaged forests are actually in use for agroforestry or for hunting and gathering. Agroforestry does reduce biodiversity, but it can also act as an effective buffer to forest clearance and conversion to other land uses, which present the greatest threat to forested ecosystems. In forests used for logging, whole-landscape management is crucial. Here, emphasis is placed on areas of intensive use interspersed with areas for conservation and catchment purposes. Management strategies for sustainable forestry are being developed, but there is a need for further interaction among foresters, ecologists, community representatives, social scientists, and economists.

Most forests of the world fall between the extremes of intensively harvested plantations and managed conservation forests. Of the ~3.54 billion ha of forested lands (about a third of Earth's land surface) (Fig. 1), about 150 million ha are plantations and another 500 million ha are classified as actively managed for goods and services (*1*, *2*). However, this is a considerable underestimate of the area of forest affected (and often dominated) by human activity as it excludes large areas affected by indigenous gardening, hunting and gathering (*3*), and indirect management such as changed fire regimes.

Human dominance of forested ecosystems continues to increase. Earth's forested estate has shrunk by about a third (2 billion ha) since the rise of agriculture-based civilizations and continues to be eroded at dramatic rates. Harvesting for wood and fuel is currently about 5 billion m^3 annually and is increasing by about 1.5% (75 million m^3) per year (*1*). In addition, some 10 million ha of new land, cleared largely from forests, is needed each year to support the increase in world population at current levels of nutritional and agricultural yields (*4*). Estimates suggest that forest clearing averaged over 13 million ha per year from 1980 to 1995, which was only partly compensated for by about 1.3 million ha per year of new plantations (*2*).

Forests are major stores of biodiversity and maintain ecosystem services critical to the biosphere as a whole. It is estimated that about 170,000 plant species, or two-thirds of all plant species of Earth, occur in tropical forests (*5*). Even in a supposedly well-collected region of Iquitos, Peru, nearly 70% of the extracted timber comes from a tree that was first described in 1976 (*6*). Forests constitute a major store of carbon [330 gigatons (1 Gt = 10^9 metric tons) in the vegetation and 660 Gt in the forest soils], and the management of forests is a major contributor to greenhouse gas budgets. Forests of mid- and high latitudes are estimated to be net sinks of carbon (0.7 ± 0.2 Gt/year), mostly because of uptake by rapidly growing young forests, whereas tropical forests are probably a large net source (1.6 ± 0.4 Gt/year), mostly because of clearing and conversion to other land uses (*7*).

Clearing of Forests

Most clearing arises from pressures that are external to the forested ecosystem. Throughout the world, there has been a history of undervaluing the forest resource; for example, royalties, purchase costs, or "stumpage" payments have often been set too low to recover the costs of management, let alone the costs of externalities. Low prices encourage land managers to liquidate the existing natural capital of the forest, replacing it with an agricultural system that yields quicker returns. This is exacerbated in societies where immediate needs predominate, which leads to a very high discount rate on future income. These same pressures have led forestry industries to "mine" the existing resource and make insufficient efforts to develop intensively managed regrowth forests, plantations, and protective management. The situation may be made worse by inappropriate interventions, such as trade bans to discourage "unsustainable harvesting," which often serve to reduce the value of the forest resource to the producing country and hasten forest exploitation. A simulation of the impacts of such a ban on Indonesia showed that internal consumption of sawlogs and plywood would increase significantly and that the rate of deforestation would be little affected (*8*).

I. R. Noble is in the Research School of Biological Sciences, Institute of Advanced Studies, Australian National University, Canberra 0200, Australia. R. Dirzo is in the Instituto de Ecología, Universidad Nacional Autonoma de Mexico, AP 70-275, Mexico City, Mexico 04510 DF.