



**Endangered Ecosystems of the United States:
A Preliminary Assessment of Loss and Degradation¹**

by

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Abstract. We report estimates of declines of natural ecosystems in the United States, provide a rationale for ecosystem-level conservation, discuss decline and threat as criteria for conservation, and relate ecosystem losses to endangerment at species and population levels. Ecosystems are defined generally and at various spatial scales and include vegetation types, plant associations, natural communities, and habitats defined by floristics, structure, age, geography, condition, and other ecologically relevant factors. The methodology for this report consisted of a literature review and a survey of conservation agencies and professionals. The results of this preliminary study indicated significant losses of biodiversity at the ecosystem level in the United States. The most substantial losses were summarized by listing ecosystems as critically endangered (>98% decline), endangered (85-98% decline), and threatened (70-84% decline). We identified more than 30 critically endangered, 58 endangered, and more than 38 threatened ecosystems. Losses of all kinds of ecosystems have been most pronounced in the South, Northeast, and Midwest, and in California.

We suggest that integrated conservation plans for all ecosystems be developed in each ecoregion of the United States, starting with types and regions that sustained the greatest losses and are at greatest risk of further loss. Conservation plans could be based on detailed studies of ecosystem status and trends and include quantitative analyses of ecosystem decline, ecological consequences of loss and degradation, and current and potential threats to each ecosystem. Ecosystem conservation need not be restricted to pristine sites, which are now almost nonexistent. Rather, management and, where possible, restoration plans for native biodiversity in partially disturbed sites should be considered.

Key words: Biodiversity, coarse filter, vegetation, gap analysis, status and trends, endangered species, conservation.

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Loss of biodiversity is real. Biologists have alerted each other and much of the general public to the contemporary mass extinction of species. Less recognized is loss of biodiversity at the ecosystem level, which occurs when distinct habitats, species assemblages, and natural processes are diminished or degraded in quality. Tropical forests, apparently the most species-rich terrestrial habitats on Earth, are the most widely appreciated, endangered ecosystems; they almost certainly are experiencing the highest rates of species extinction today (Myers 1984, 1988; Wilson 1988). However, biodiversity is being lost more widely than just in the tropics. Some temperate habitats, such as freshwaters in California (Moyle and Williams 1990) and old-growth forests in the Pacific Northwest (Norse 1990) to name but two, are being destroyed faster than most tropical rainforests and stand to lose as great a proportion of their species. Because so much of the temperate zone has been settled and exploited by humans, losses of biodiversity at the ecosystem level have been greatest there so far.

Ecosystems can be lost or impoverished in basically two ways. The most obvious kind of loss is quantitative--the conversion of a native prairie to a corn field or to a parking lot. Quantitative losses, in principle, can be measured easily by a decline in areal extent of a discrete ecosystem type (i.e., one that can be mapped). The second kind of loss is qualitative and involves a change or degradation in the structure, function, or composition of an ecosystem (Franklin et al. 1981; Noss 1990). At some level of degradation, an ecosystem ceases to be natural. For example, a ponderosa pine (*Pinus ponderosa*) forest may be high-graded by removing the largest, healthiest, and frequently, the genetically superior trees; a sagebrush (*Artemisia* spp.) steppe may be grazed so heavily that native perennial grasses are replaced by exotic annuals; or a stream may become dominated by trophic generalist and exotic fishes. Qualitative changes may be expressed quantitatively, for instance, by reporting that 99% of the sagebrush steppe is affected by livestock grazing, but such estimates are usually less precise than estimates of habitat conversion. In some cases, as in the conversion of an old-growth forest to a tree farm, the qualitative changes in structure and function are sufficiently severe to qualify as outright habitat loss.

Biologists agree that the major proximate causes of biotic impoverishment today are habitat loss, degradation, and fragmentation (Ehrlich and Ehrlich 1981; Diamond 1984; Wilson 1985; Wilcox and Murphy 1985; Ehrlich and Wilson 1991; Soulé 1991). Hence, modern conservation is strongly oriented toward habitat protection. The stated goal of the Endangered Species Act of 1973 is "to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved" (P.L. 94-325, as amended). The mission of The Nature Conservancy, the largest private land-protection organization in the United States, is to save "the last of the least and the best of the rest" (Jenkins 1985:21) by protecting natural areas that harbor rare species and communities and high-quality samples of all natural communities.

Despite the many important accomplishments of natural-area programs in the United States, areas selected under conventional inventories tend to be small. As predicted by island biogeographic theory (MacArthur and Wilson 1967) and, more generally, by species-area relationships, smaller areas tend to have fewer species. All else being equal, smaller areas hold smaller populations, each of which is more vulnerable to extinction than larger populations (Soulé 1987). Recognizing that small natural areas that are embedded in intensively used landscapes seldom maintain their diversities for long, scientists called for habitat protection and management at broad spatial scales such as landscapes and regions (Noss 1983, 1987, 1992; Harris 1984; Scott et al. 1991a, 1991b). In practice, however, most modern conservation continues to focus on local habitats of individual species and not directly on communities, ecosystems, or landscapes (Noss and Harris 1986).

Ecosystem conservation is a complement to--not a substitute for--species-level conservation. Protecting and restoring ecosystems serve to protect species about which little is known and to provide the opportunity to protect species while they are still common. Yet, ecosystems remain less tangible than species (Noss 1991a). And although the logic behind habitat protection as a means of conserving biodiversity is difficult to refute, conservationists face a major hurdle: convincing policy makers that significantly more and different kinds of habitat must be designated as reserves or otherwise managed for natural values. Scientists cannot yet say with accuracy how much land or what percentage of an ecosystem type must be kept in a natural condition to maintain viable populations of a given proportion of the native biota or the ecological processes of an ecosystem. However, few biologists doubt that the current level of protection is inadequate. Estimates of the fraction of major terrestrial ecosystem types that are not represented in protected areas in the United States range from 21 to 52% (Shen 1987). Probably a smaller percentage is adequately protected. For example, 60% of 261 major terrestrial ecosystems in the United States and in Puerto Rico, defined by the Bailey-Kuchler classification, were represented in designated wilderness areas in 1988 (Davis 1988). Only 19% of those ecosystem types, however, were represented in units of 100,000 ha or more and only 2% in units of 1 million ha or more--all of them in Alaska (Noss 1990). Because the size of an area has a pronounced effect on the viability of species and on ecological processes, representation of ecosystem types in small units, in most cases, cannot be considered adequate protection.

Inadequate protection can be put in perspective by the extent of lost biodiversity at the ecosystem level and by the correlation of these losses with losses at other levels of biological organization. To this end, we report estimates of the extent to which natural ecosystems (vegetation, natural communities, or habitat types) in the United States have declined, provide a rationale for the strategy of ecosystem-level conservation, discuss decline and threat as criteria for conservation, and relate ecosystem losses to declines at species and population levels. We emphasize terrestrial and wetland ecosystems because quantitative declines of these types have been reported most extensively. We also address losses of aquatic ecosystems (primarily lakes and streams) for which fewer statistics are available and examples of losses of nearshore marine ecosystems, although these systems were poorly represented in the literature.

While we acknowledge the preliminary nature of our data and analysis, our results indicate that more biodiversity at the ecosystem level has been lost than is generally recognized in environmental-policy debates. A continually expanding list of endangered species seems inevitable unless trends of habitat destruction are reversed soon through a national commitment to ecosystem protection and restoration. A strategy for ecosystem conservation must not only protect and restore ecosystem types that are already endangered but must be proactive by conserving multiple, healthy examples of all native ecosystem types in each region (Tear et al. 1993). We are encouraged that the National Research Council (1993) in its recommendations to the National Biological Service emphasized the need to develop a functional ecosystem classification, to inventory imperiled ecosystems, and to identify ecosystems that are most in need of restoration.

We invite readers of this report to send additional, pertinent data on loss and degradation of ecosystems to R. Noss, (University of Idaho, Department of Fish and Wildlife, Moscow, Idaho 83844) so that this report may be updated.

Definitions

The term ecosystem is generally used to denote a community of all the species populations that occupy a given area and its nonliving environment (Odum 1971). Species distributions respond to environmental gradients in time and space in a way that is often individualistic. However, for conservation, the identification of ecosystems as reasonably discrete entities that can be delineated and mapped is worthwhile. An ecosystem can be a vegetation type, a plant association, a natural community, or a habitat defined by floristics, structure, age, geography, condition, or other ecologically relevant factors. Thus, virgin and old-growth forests, pitcher plant (*Sarracenia* spp.) bogs, un-grazed sagebrush steppe, wetlands (general or specific types), Midwestern oak (*Quercus* spp.) savanna, vernal pools, free-flowing rivers, and seagrass meadows are ecosystem types. Our

concept of ecosystem is hierarchical because broad vegetation types subsume many plant associations and habitats. We found the generality of our definition useful because it allows assessment of loss or degradation of structural, functional, or compositional aspects of ecosystems (Franklin et al. 1981; Noss 1990) at any level of the classification hierarchy and at any spatial scale. A rigorous, consistent classification of ecosystems--although useful for other purposes (Bourgeron 1988; Orians 1993)--could easily hide changes in ecosystem parameters that are not included in type definitions. For example, loss of old-growth forests, vernal pools, or free-flowing rivers could not be evaluated from a classification by floristic criteria (such as Poore 1955; Daubenmire 1968). More useful is the natural-community classification system used by The Nature Conservancy, in which types are defined by a combination of physical habitat, vegetation, physiognomy, and species composition. Even here, qualities such as un-grazed, virgin, old-growth, and other adjectives important to conservation are not included in classifications but must be added as attributes of site descriptions. Thus, we opted for an inclusive approach in defining ecosystems.

Methods

Our central research question was--to what extent have natural ecosystems in the United States been reduced in area or degraded in quality by human activities? Our methodology consisted of a literature review and a survey of conservation agencies and professionals. Although this approach was laborious and crude and depended on data of highly variable quality, a more systematic approach at a national scale is not yet possible. No accurate maps or other data showing vegetation of the United States before European settlement and at present are available. An earlier national assessment (Klopatek et al. 1979) was based on a county-by-county comparison of Conservation Needs Inventory land-use data from 1967 and a map of potential natural vegetation (Kuchler 1966). The results were informative about general trends but of low resolution. Furthermore, as acknowledged by Klopatek et al. (1979), the Kuchler map has many limitations and inaccuracies, in part because of assumed climax conditions and an absence of natural disturbances. For example, the Southeastern Coastal Plain is shown by Kuchler (1966) as predominantly southern mixed forest (*Fagus-Liquidambar-Magnolia-Pinus-Quercus*), whereas in reality, it was dominated by longleaf pine (*P. palustris*) before European settlement because of the high frequency of natural ignitions, perhaps supplemented by fires set by Native Americans (Bartram 1791; Harper 1914; Noss 1988, 1989; Ware et al. 1993; Schwartz 1994).

The Gap-Analysis Project of the National Biological Service uses state-by-state maps of current vegetation, including anthropogenic habitat types generated from LANDSAT thematic mapper imagery and ancillary data (Scott et al. 1993). However, complete national coverage will not be available for several years. Maps of presettlement vegetation exist for only some states. We originally hoped to produce a digital comparison of Kuchler potential natural vegetation types (corrected for inaccuracies) and current land-use/land-cover maps from the U.S. Geological Survey, but this was impossible because the latter maps have not been edge-matched for national coverage. An additional problem is that vegetation maps tell nothing about certain kinds of ecosystems, including aquatic types. Because of these constraints, a survey of literature, conservation agencies, and biologists was the only means of obtaining a reasonably comprehensive picture of ecosystem losses nationally.

Not only are nationwide maps of presettlement and current vegetation lacking, but comprehensive nationwide monitoring of ecosystems does not exist. The National Wetlands Status and Trends reports of the U.S. Fish and Wildlife Service (Dahl 1990; Dahl and Johnson 1991) provide statistically reliable data on wetlands as generally defined, but not on specific wetland plant communities; furthermore, these reports do not address qualitative changes in wetlands. The Environmental Monitoring and Assessment Program of the U.S. Environmental Protection Agency (Hunsaker and Carpenter 1990)--many years under development but still not fully functional--also fails to monitor the statuses of specific vegetation types or habitats in a manner useful for our purposes. Thus, our assessment had to rely on published and unpublished data from many sources.

Published estimates of the extent to which ecosystems in the United States have declined in area or quality are scattered and anecdotal; there are no key words for easy literature searches. However, we collected articles on ecosystem decline from multiple sources since 1982 and made comprehensive searches (skimming all articles

with promising titles) of *Conservation Biology* (all issues; 1987-93), *The Nature Conservancy News-The Nature Conservancy Magazine-Nature Conservancy* (1980-93), *Natural Areas Journal* (all issues; 1981-93), and *Restoration and Management Notes* (all issues; 1981-93). We also scanned titles of *Biological Conservation*, *BioScience*, *Ecology*, and *Environmental Management* during the most recent 14 years (1980-93).

To supplement the literature search, we sent requests for information and citations on ecosystem loss and degradation to the natural-heritage programs in the 50 states. These programs, now mostly incorporated in state agencies, were initiated by The Nature Conservancy beginning in 1974 and usually represent the best single source of information on biodiversity, particularly rare species and communities in each state (Jenkins 1985, 1988; Noss 1987). The requests to the heritage programs were mailed in September 1992; follow-up letters to program managers that had not responded were mailed in December 1992. By 1 March 1993, 37 (73%) of the 51 state-heritage program managers (Pennsylvania has 2) had responded; 5 stated they had no information, and 32 provided data of some type. Information included literature citations, copies of articles and reports, internal documents, and unpublished estimates of ecosystem losses by heritage ecologists and other experts. In some cases, heritage ecologists could provide only state and global ranks for a natural community from The Nature Conservancy's ranking system. These ranks are usually based more on rarity than on extent of loss or vulnerability to future loss. However, the material from the heritage programs was invaluable; much of it could not reasonably have been obtained in any other way. On referral by many programs, we contacted other scientists doing work on declining ecosystems. We also contacted professionals in other state and federal agencies when we had reason to believe they had data on ecosystem declines.

Results

As anticipated, estimates of ecosystem decline (Appendix A) from published sources and heritage programs correspond to no consistent classification, level of classification hierarchy, or spatial scale. Data for estimates were collected in different ways, and some estimates were simply best guesses by experts familiar with a state or region. We listed the best documented or most recent estimated losses of each ecosystem type (Appendix A). If two or more estimates for the same or similar type conflicted but were reasonably credible, we reported all or a range (e.g., 50-75% loss). All estimated losses of more than 50% are reported; additionally, many losses of less than 50% (including all statewide wetland losses) are shown for comparison. Variation in quality of estimates could not be assessed objectively; however, independent estimates of decline for a given type usually converged closely, suggesting that serious errors were infrequent. For example, apparently independent estimates of tallgrass-prairie losses in Midwestern states were almost identical (Appendix A).

Ecosystem types that seem to be most endangered in the United States--as measured by areal loss or ecological degradation--are divided into three classes (*critically endangered*, *endangered*, and *threatened*) by percentage of decline (Appendix B). The ecosystems we classified as critically endangered, endangered, and threatened are arranged by major habitat type (Fig. 1). Bearing in mind that ecosystems at several levels of a hierarchical classification and spatial scale are lumped in our analysis, 57% of the ecosystems that have declined by over 70% are terrestrial, 33% are wetland, and 10% are aquatic (including all major rivers in each of seven regions as ecosystem types; Fig. 1A). Forest, grassland, and savanna communities dominate the list, especially in the critically endangered category (Fig. 1B).

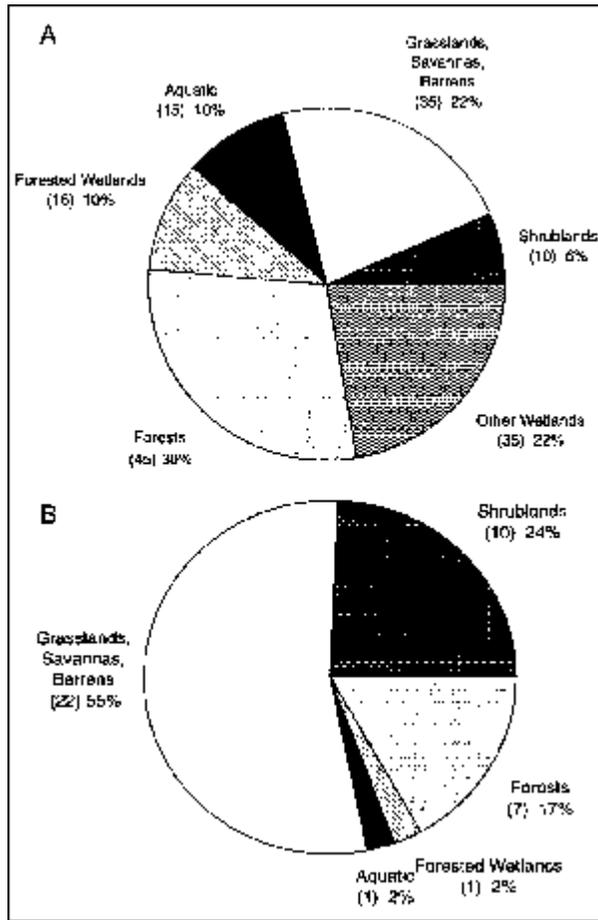


Fig. 1.

among grassland, savanna, and barrens communities.

The greatest number of estimates and the greatest extent of losses are in the Northeast, South, Midwest, and California (Fig. 2) and may reflect the more intensive land uses in these regions, earlier settlement by Europeans, and more intensive scientific study. Absence of estimates from a state, region, or particular type of ecosystem reflects an absence of data but does not imply that no losses have occurred there. Heritage-program ecologists in some states were more willing than in others to estimate ecosystem declines in the absence of quantitative data.



Fig. 2. Distribution of critically endangered, endangered, and threatened ecosystem types by geographic region (defined ad hoc for this study; Appendix B). Each region received a point when types overlapped regions. Regions with fewer types are not necessarily in better condition because numbers reflect programs.

Although our results are preliminary, each estimate of ecosystem decline serves as an hypothesis that potentially can be falsified, corrected, or verified by subsequent research. We hope the estimates tallied here will stimulate

status surveys and other research that will lead to rigorous statistics on ecosystem declines and current threats.

Discussion

The natural ecosystems of the United States have been significantly altered. We found endangered ecosystems at several levels of classification and at many spatial scales. Although losses of major regional vegetation types may have greater implications for biodiversity than losses of local plant associations, declines at any level represent depletion of biodiversity worthy of concern from conservation agencies. With more intensive documentation of losses, we expect lists of endangered ecosystems to expand and to become dominated by communities at lower levels of classification (for example, plant associations as opposed to vegetation alliances or formations) as types are more narrowly distinguished. As suggested by Orians (1993), a coarser classification would result in the identification of fewer sites as needing protection. Thus, conservation agencies may expect political pressure to keep classifications coarse (Orians 1993). However, hierarchical classifications with finely distinguished types are necessary to encompass the range of natural variation in ecosystems.

Ecosystems as Targets of Conservation

Ecosystem conservation offers several advantages over a species-by-species approach for the protection of biodiversity: it directly addresses the primary cause of many species declines (habitat destruction), it offers a meaningful surrogate to surveying every species, and it provides a cost-effective means for simultaneous conservation and recovery of groups of species. The species-by-species approach--although extremely important to our efforts of saving biodiversity--is inefficient (LaRoe 1993). As the public becomes more familiar with the evidence that entire ecosystems or groups of species have declined and that saving individual species under the Endangered Species Act of 1973 does not solve all conservation problems and does not necessarily prevent the need for future listings, the rationale for ecosystem conservation becomes more compelling.

The idea of representing examples of all ecosystems in protected areas extends back to the nineteenth century in Europe and in Australia and to the early twentieth century in North America. Early efforts to preserve a broad spectrum of natural communities in North America were led by two related committees of the Ecological Society of America: the Committee on the Preservation of Natural Conditions and the Committee on the Study of Plant and Animal Communities (Ride 1975; Noss and Cooperrider 1994). In 1926, the first committee published the *Naturalist's Guide to the Americas* of nature sanctuaries in North America for representing ecosystems, emphasizing sufficiently large and pristine areas to maintain large mammals (Shelford 1933; Kendeigh et al. 1950-51). In 1946, the Committee for the Preservation of Natural Conditions separated from the Ecological Society after a controversial decision that the society should not be involved in conservation advocacy and became a separate organization, the Ecologists' Union. In 1950, this group was reorganized as The Nature Conservancy, named after a British organization with similar goals (McIntosh 1985).

The Nature Conservancy calls its community-level conservation strategy a coarse filter (Noss 1987) and has estimated that 85-90% of species can be protected by conserving samples of natural communities without separate inventory and management of each species. A coarse-filter strategy can be implemented at any desired level of a hierarchical classification, including landscape types based more on vegetation or physical habitat pattern than on species composition (Noss 1987). Species not effectively captured by a coarse filter, such as narrow endemics or large carnivores, can be addressed through the conventional fine filter of rare-species inventory and protection. The coarse filter has received less attention than species-level protection from The Nature Conservancy and from almost all conservation agencies during the last 3 decades. However, interest in coarse filters was recently renewed because of concerns about the low efficiency and high cost of species-by-species approaches under the U.S. Endangered Species Act (Kohm 1991; LaRoe 1993).

One limitation of the coarse-filter strategy is that plant and animal communities are not stable for long periods;

they change as species respond independently to environmental gradients in space and time. When climate changes, species respond differently to shifting habitat conditions at rates determined by their dispersal capacities and other aspects of autecology (Davis 1981). Some biologists have suggested that an ideal representation of all ecosystems would be a full array of physical habitats, environmental gradients, and landscape patterns in reserves rather than vegetation or other biotic communities (Noss 1987, 1992; Hunter et al. 1988; Hunter 1991). Canada has embarked on a gap-analysis project to assess representation of enduring features of landscapes in reserves in each defined ecoregion (World Wildlife Fund Canada 1993). Enduring features include landforms, soils, and other physical qualities that are more persistent than vegetation, particularly in glaciated regions. However, in the United States, existing classifications, inventories, and maps of terrestrial ecosystems are based primarily on vegetation. Development of physical habitat-based maps is not an urgent need when vegetation can be accurately mapped. In the short term at least, vegetation is often a good surrogate for overall biodiversity (Crumpacker et al. 1988; Scott et al. 1991a, 1991b, 1993).

One of the most compelling arguments for a coarse-filter or ecosystem approach is its efficiency and cost-effectiveness. Single-species conservation has failed in many ways (Noss and Harris 1986; Hutto et al. 1987; Scott et al. 1987; Hunter 1991; Noss 1991a). A major limitation is that most species conservation is essentially reactive. Unless a species is of great commercial or recreational importance, such as a game animal, little effort is made to protect or even manage it until it becomes so rare that extinction is imminent. At this point, protection and recovery may be expensive and require immediate and extreme changes in land use, which may be fiercely opposed by economic interest groups. Many endangered-species conflicts that polarize society today--such as that over the northern spotted owl (*Strix occidentalis caurina*)--arguably could have been prevented if land-managing agencies had taken steps to protect adequate amounts and distributions of habitat before populations declined to where listing was legally required. This hindsight comes too late for the owl, which now must be managed intensively at great cost, but may help persuade agencies and political bodies elsewhere to start protecting ecosystems before the species associated with them become threatened or endangered.

Many ecosystems provide resources for large numbers of federally listed and candidate species (Appendixes C-E). Improving conservation of these and other endangered ecosystems will likely promote the protection and restoration of populations of imperiled species. A holistic plan for each ecosystem would require much work but would almost certainly be less costly in time and money than an uncoordinated series of recovery plans and habitat-conservation plans for each individual species. More importantly, ecosystem conservation may reconcile conflicts between separate management strategies for individual species.

Ecosystem conservation does not remove the need to understand the autecology and the protection requirements of individual species and certainly does not preclude the need for the Endangered Species Act of 1973; but the act can be strengthened to improve protection and prospects of recovery of species and ecosystems (Murphy et al. 1994). The species remains the central level of organization. Ecosystems are often defined by their species, and details of ecosystem management such as optimal patch size, spacing, and connectivity must be addressed with reference to species that are vulnerable to human activities. Furthermore, many species have become so rare that they require individual attention (including listing and recovery planning) to avert extinction (Atwood and Noss 1994). But as a general strategy, the top-down planning of ecosystem conservation is a strong complement to a species-by-species approach, if for no other reason than the inability of the species approach to prevent additional species from declining to threatened or endangered status (Noss and Cooperrider 1994).

The Natural Community Conservation Planning Process of California is an example of attempted conservation at an ecosystem level by a state government. The process was authorized by state legislation, the Natural Community Conservation Planning Act of 1991 (Fish and Game Code Section 2800 et. seq.), which was intended to promote cooperation among landowners, conservationists, developers, urban planners, government, and other parties in land-use planning (California Environmental Trust 1992, California Resources Agency 1992). The pilot project of the Natural Community Conservation Planning is the conservation of the southern California coastal sage scrub, a community type that is already depleted by 70-90% (Atwood 1990); the plan is being developed under the guidance of a governor-appointed scientific review panel and other experts.

Landowners can voluntarily enroll their properties in the program, obtain state approval for developments that do not conflict with conservation objectives, and hopefully avoid the costly delays and court battles that have become commonplace in this species-rich and rapidly urbanizing region. However, only about 15% of the remaining coastal sage scrub in the three major counties (Orange, San Diego, and Riverside) in the planning area is enrolled in the Natural Community Conservation Planning process (U.S. Fish and Wildlife Service 1993; Atwood and Noss 1994), which arguably is not enough to assure successful implementation of the regional conservation plans. Additional incentives may be required to persuade enrollment by landowners.

The motivation for the Natural Community Conservation Planning clearly was to reduce political conflicts generated by proposed endangered-species listings. The main force driving the Natural Community Conservation Planning was concern over the economic effects of listing the California gnatcatcher (*Polioptila californica*); the species was listed as threatened by the U.S. Fish and Wildlife Service in March 1993 (U.S. Fish and Wildlife Service 1993) but was delisted only 1 year later over a technicality (New York Times, 4 May 1994) and then was relisted. The endangered Stephen's kangaroo rat (*Dipodomys stephensi*) is also associated in part with coastal sage scrub. An additional 33 animal and 61 plant species associated with the community are considered sensitive (Scientific Review Panel 1992); 53 of them are candidates for federal listing (Appendix D). The gnatcatcher is, however, still not a candidate for listing at a state level; listing has been considered premature during the Natural Community Conservation Planning process. The California Resources Agency promotes the Natural Community Conservation Planning as a way to "avoid the eleventh-hour crises that force choices between losing species and shutting down regional economies" (Mantell 1992:1) and emphasizes the desirability of ecosystem-level planning over the regulatory approach of the Endangered Species Act of 1973. Many environmentalists have been skeptical of the state's motives. Some have condemned the Natural Community Conservation Planning, especially because it lacks effective interim control and leaves many crucial decisions to local authorities (Silver 1992). Many observers now agree that listing the gnatcatcher was the force that finally moved the Natural Community Conservation Planning forward (Atwood and Noss 1994).

To be more effective, agencies could also develop conservation plans for common and widespread natural communities or ecosystems, not only for those already in jeopardy. Ideally, integrated conservation plans should be developed for all ecosystem types in each ecoregion. By the time an ecosystem declines to a fraction of its former size (Appendix B), the major advantages of ecosystem conservation--proactive avoidance of conflict, cost-effectiveness, efficiency--have been compromised. Many species (Appendixes C-E) are already rare enough that intensive efforts--the kind of action fostered by the Endangered Species Act of 1973--are required to restore their viability. Ecosystem-level planning for endangered communities may prevent some species from declining to where listing is necessary but probably does not suffice for species that are already on the brink of extinction. Where possible, ecosystem conservation must be implemented before threats become imminent.

Decline and Threat as Conservation Criteria

Conservationists commonly cite statistics about declines of species and ecosystems. Yet, extent of decline is not a common criterion for evaluating areas for conservation; more common criteria are diversity, rarity, naturalness, area, threat of human interference, amenity or educational value, representativeness, and others (Margules and Usher 1981; Usher 1986). The Nature Conservancy bases its conservation proposals mostly on rarity, particularly at the species level (Noss 1987). The Nature Conservancy and state heritage programs rank elements at global and state scales. States differ somewhat in their interpretation of global ranking (G) criteria; when applied quantitatively (e.g., California Natural Diversity Data Base, unpublished), the criteria are:

G1 = Less than 6 viable element occurrences or less than 1,000 individuals or less than 2,000 acres.

G2 = 6-20 element occurrences or 1,000-3,000 individuals or 2,000-10,000 acres.

G3 = 21-100 EOs or 3,000-10,000 individuals or 10,000-50,000 acres.

G4 = Apparently secure; this rank is clearly lower than G3 but factors exist to cause some concern; i.e., there is

some threat, or somewhat narrow habitat.

G5 = Population demonstrably secure to ineradicable due to being commonly found in the world.

Other ranks may be assigned to historical occurrence, presumed extinction, questionable taxonomic status, and other statuses (Master 1991a). State ranks are usually based on identical numerical criteria except that the status of each element is considered separately within each state's boundaries. Thus, elements (species or community types) are ranked primarily according to population size, number of occurrences (populations or locations), or size of area; differences between statuses before and after human settlement and threats from current trends are not recognized. However, The Nature Conservancy's Element Global Ranking Record often contains information on trends, threats, and fragility (Master 1991a) that may influence rankings. Furthermore, some states modified global and state ranking criteria to identify threats or declines. The California Natural Diversity Data Base (unpublished documents) divides rankings of 1, 2, or 3 into three categories, for example, S1.1 = very threatened, S1.2 = threatened, and S1.3 = no currently known threats. In New Jersey, state ranks include extent of decline as a criterion. The definition for S1 species includes the statement: "Also included are elements which were formerly more abundant, but now through habitat destruction or some other critical factor of its biology have been demonstrably reduced in abundance" (Breden 1989: Appendix 3, page 2; Grossman et al. 1994). In practice, however, rarity ranks more prominently than extent of decline because "gathering information on the 'extent of decline' of a natural community type is a difficult task. It is easier to describe what we have now than to figure out what we once had" (T. F. Breden, New Jersey Department of Environmental Protection, Division of Parks and Forestry, Trenton, N.J., personal communication). The Nature Conservancy has few global ranks for communities because the heritage programs "haven't yet reconciled the state community classifications into a compatible overall national or international system" (Master 1991a:562).

We suggest that heritage programs, other agencies, and researchers of rare communities determine whether the rarity of these communities preceded European settlement or is a recent consequence of human activity. Outside the historic context, rarity may not be a meaningful conservation criterion. Some rare species and communities are not in serious jeopardy. For example, a localized limestone outcrop of a few hectares may have held an unusual community of endemic plants since the Pleistocene, has not changed much since then, and is under little threat today. On the other hand, an old-growth forest of 1,000 ha today may have once covered millions of hectares; furthermore, it may be scheduled for cutting. But under traditional heritage-program criteria, conservation of the outcrop is given higher priority.

Another important contextual consideration for conservation on a state scale is the entire geographic range of a community or species. In the former example, if the outcrop community occurs only in Pennsylvania but the old-growth forest was widespread across the eastern United States, the order of priority for conservation would be reversed, regardless of the status and trends of the two communities in the state. The Nature Conservancy (Master 1991a) recognizes the problem of scale by giving higher priority to global than state rankings. However, not all state governments recognize trends beyond their boundaries and may be extremely provincial in their decisions. In many states, characteristic regional vegetation types have suffered massive declines, yet, agencies do not consider them of high priority for protection. Instead, agencies often focus on the curiosities, such as relict or peripheral community types that were never common. For example, the natural-areas program of the Ohio Department of Natural Resources devotes more attention to bogs, fens, and other Pleistocene relics that can be managed conveniently in small reserves as living museums than to the forest ecosystems that once dominated the state (R. Noss, personal observation). Forest area in Ohio recently increased to about twice its value in 1939-42 but is still only 27% of the state, whereas it was more than 95% before European settlement (Good 1979; King 1990). The secondary forests, mostly in the Appalachian Plateau of Ohio, are heavily fragmented by roads, gas pipelines, unreclaimed strip mines, clear-cuts, and other intrusions. Like most second-growth forests, they are structurally impoverished compared to old-growth forests. Only some small patches of old-growth forest remain in Ohio (Good 1979).

Noss (1988, 1991a) suggested that extent of decline may be preferable to rarity as a primary criterion for conservation. Many rare species and communities are restricted because of natural reasons such as localized

habitat conditions rather than human disturbance. Many rare plants have been confined to small areas throughout their histories (Holsinger and Gottlieb 1991; Simberloff 1991) and can be expected to have adapted to inbreeding and isolation and to not be highly vulnerable to extinction (Huenneke 1991). Furthermore, the ecological roles of such species are usually minor. On the other hand, a significant decline in a once-dominant or keystone species could have profound ecological ramifications, including alteration of interspecific interactions across foodwebs, disruption of nutrient cycling or disturbance regimes, and other perturbations. These ecosystem-wide effects could occur long before a pivotal species becomes rare enough for listing as endangered. We suggest that the same problems may occur when once-dominant ecosystems--many of them identified by their dominant or characteristic species--suffer major declines. Declines of ecosystems are directly contrary to what may be the best accepted and most widely applicable conservation criterion of all: adequate representation of all ecosystem types (Dasmann 1972; UNESCO 1974; McNeely and Miller 1974; Austin and Margules 1986; Nilsson 1986; Scott et al. 1993).

The extent to which various ecosystems have declined in the United States--despite uncertainties and unevenness in the data--portrays a striking picture of endangerment (Appendixes A, B). The next crucial step is the determination of the relative risks of further losses. Threat or vulnerability is widely acknowledged in the academic literature as a major consideration for conservation evaluation. As Diamond (1976:1028) stated, "conservation strategy should not treat all species as equal but must focus on species and habitats threatened by human activity." Although not emphasized in The Nature Conservancy's global ranking system, degree of threat is commonly used at a state level for the evaluation of alternative sites for conservation.

The Endangered Species Act of 1973 strongly bases decisions about listing on threat. Factors in the determination of listing a species include "(A) the present or threatened destruction, modification, or curtailment of its habitat or range; (B) overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) the inadequacy of existing regulatory mechanisms; (E) other natural or manmade factors affecting its continued existence" (P.L. 94-325 as amended, Sec. 4 (a), p. 4). The U.S. Fish and Wildlife Service uses a 12-point ranking system for determining listing priorities first by magnitude (high or moderate to low) and by immediacy (imminent or nonimminent) of threat and secondarily by taxonomic distinctness (e.g., monotypic genus, species, or subspecies). A separate 18-point scale by degree of threat, recovery potential, taxonomic distinctness, and conflict with economic objectives is used to rank species for funding of recovery (Fay and Thomas 1983; Master 1991a).

We recommend that analogous criteria be applied to ecosystems for determining priorities for conservation. The taxonomic-distinctness criterion may be applied by focusing on unique ecosystems--ecosystems that are most different from other types in species composition or structure. However, because of the many undescribed and unknown species, we believe that distinctness should remain secondary to magnitude and immediacy of threat for setting priorities. An initial focus on ecosystems that have declined greatly (Appendix B) makes sense because degree of threat often correlates with extent of decline. Old-growth forests, for example, have declined greatly because their timber is economically valuable (Noss 1990); that same value puts remaining unprotected stands at high risk. If remaining stands are granted legal protection--as conservationists propose--that threat would be largely removed (although poaching of timber may become a problem in some areas). Prairies, other grasslands, and savannas have dwindled throughout the United States (C. Madsen 1989; Appendix A) because their soils are typically fertile and tillable; remnant native grasslands are obvious priorities for protection. But protection need not be restricted to pristine or near-pristine sites. Degraded examples of endangered ecosystems may warrant more attention than high-quality examples of ecosystem types that have suffered less severe losses and are not faced with an imminent threat; such decisions are best made case-by-case with consideration of many factors. Communities that receive partial regulatory protection, such as wetlands (Cabbage et al. 1993; Water Environment Federation 1993), are often at lower risk than uplands, which lack such protection.

Some current or future risks may not strongly correlate with past declines because human settlement is expanding into new areas or because technologies allow exploitation of undisturbed habitats. For example, The Nature Conservancy ranks the Pocono till barrens and serpentine barrens, which contain the largest and second largest concentrations of terrestrial endangered species in Pennsylvania, (plant and animal) as G1 and G2 (R.

Latham, University of Pennsylvania, Philadelphia, personal communication). These localized communities have declined by an estimated 10-50% and therefore would not be considered endangered or threatened ecosystems under our criteria. However, these communities are now under severe threat in some areas. As Latham (R. Latham, University of Philadelphia, personal communication) stated:

"Until recently, serpentine barrens have enjoyed a modest level of natural protection: the soils are poor for growing crops and they usually fail to meet percolation requirements for septic tank construction. But newer high density developments and the gradual coalescence of the suburban patchwork make sewer systems economically feasible. Equipped with sewers and treatment plants, serpentine barrens suddenly become developable. A hospital administration is currently building a nursing home atop one of the two remaining barrens in Delaware County, Pennsylvania, which once harbored at least nine such sites."

The combination of past decline and current or future risk provides a powerful criterion for evaluating ecosystems for protection. We advise that private, state, and federal conservation agencies keep track of trends and impending threats to ecosystems so that degree of threat can be included as an additional criterion for listing ecosystems as threatened or endangered. Our list of threatened and endangered ecosystems (Appendix B) should be scrutinized to determine which of these types are at greatest current risk; this determination can be used to prioritize conservation actions.

We defined decline to include degradation of ecosystem structure, function, or composition (Franklin et al. 1981; Noss 1990) as well as areal losses of an ecosystem. The measurement of qualitative changes in ecosystems is more difficult than the measurement of mapped declines in area, but qualitative changes are often more insidious (Appendixes A, B). Only about 10% of the sagebrush (*Artemisia* spp.) steppe of the Intermountain West has been converted to other habitat types, chiefly dryland or irrigated agriculture (West, in press). By this measure, sagebrush steppe is not endangered. However, sagebrush steppe has been substantially altered by livestock grazing, disrupted fire regimes, and exotic species invasions. More than 99% of the sagebrush steppe has been affected by livestock, and about 30% has been heavily grazed, resulting in dominance by a few woody plants (West, in press). Although they usually are not pristine, sites that still retain high richness of native species should receive preferential protection.

Other examples of qualitative decline are spruce-fir (*Picea rubens-Abies fraseri*) forests at high elevations in the southern Appalachian Mountains. Only about 35-57% of the spruce-fir area is lost (Boyce and Martin 1993), but almost 100% of the forest is seriously affected by the exotic balsam woolly adelgid (*Adelges piceae*), which attacks Fraser fir (Pyne and Durham 1993). Air pollution and global warming are possible causes of mortality and declined growth of red spruce (*Picea rubens*) in the region, but the effects are difficult to separate from natural causes (White et al. 1993).

Conifer forests that depend on frequent fire, notably longleaf pine in the Southeast and ponderosa pine in the West, have declined not only from logging but also from increases in tree density and from invasion by fire-sensitive species after fire suppression (Means and Grow 1985; Noss 1988; Habeck 1990; Eastside Forests Scientific Society Panel 1993). These kinds of change can cause the loss of a distinct ecosystem as surely as if the forest were clear-cut. Ecological processes are also affected; widespread insect infestation and tree mortality east of the Cascade Mountains in the Pacific Northwest is blamed largely on past fire suppression (Gast et al. 1991; Eastside Forests Scientific Society Panel 1993).

Aquatic communities offer some of the most obvious examples of qualitative degradation. The published and unpublished literature contains less discussion of biotic impoverishment at the ecosystem level for aquatic communities than for terrestrial and wetland communities, perhaps because aquatic-ecosystem degradation is qualitative and difficult to map. The statistics we found, however, are striking. For instance, 98% of an estimated 5.2 million km of streams in the conterminous United States is degraded enough to be unworthy for federal designation as wild or scenic rivers (Benke 1990). Only 3.9% of the nation's streams is considered to have maximum ability to support populations of sport fishes and species of special concern (Judy et al. 1984). Eighty-one percent of the nation's fish communities are adversely affected by poor water quality and other

threats (Judy et al. 1984). Many western streams are now dry during part of the year because of water withdrawals, primarily for agriculture. Because of declines in water quality or water quantity, 10% of the freshwater mussel species in North America have gone extinct since 1900, and 73% of the remaining species are rare or imperiled (Master 1990, 1991b). Sixty-two species of endemic aquatic snails in the Coosa River in Alabama are thought to be extinct (Palmer 1985). To the casual observer, the riverine habitat still exists; its degradation is often apparent to only those who know aquatic ecology.

We do not advocate an abandonment of concern for rare species and communities with a shift in focus to ecosystem loss, degradation, and threat. Identification and protection of rarities are essential to conservation, even if rarities have not yet experienced significant losses. A small decline may push a rare species over the brink of viability; all else being equal, small populations are more vulnerable to extinction (Shaffer 1981; Soulé 1987). Most rare species, especially plants, are local endemics typical of localized and unusual habitats (Stebbins 1980). Many of these habitats are unproductive and have so far escaped destruction. But because they are localized, they could be destroyed quickly by incompatible human activities or natural catastrophes. For example, the vernal pools of southern California, which harbor many endemic species, are simply graded over for development. Less than 4% of an original 37,000 vernal pools remain in San Diego County (Jones and Stokes 1987; Oberbauer 1990).

Environmental Correlates of Ecosystem Decline

Because of limitations and probable biases of available data, we did not conduct a comprehensive analysis of correlates of ecosystem decline. The general kinds of ecosystems identified in this study as particularly endangered (Appendix B, Fig. 1) were recognized earlier as suffering major declines (Klopatek et al. 1979). We found endangered ecosystems in all major regions of the United States except in Alaska (Fig. 2). Their concentration in eastern states probably reflects a longer history of European settlement, more complete databases, and more active, better staffed heritage programs. Thus, our illustrations (Figs. 1 and 2) reflect biases and real trends in the database and the need for greatly expanded inventories and assessments of ecological conditions in all regions. As noted earlier, these lists of endangered ecosystems contain hypotheses to test. Although we probably left out many ecosystems that are truly endangered (Appendixes A, B) but for which no credible estimates of decline are available, we do not doubt that all we list are in need of protection.

Further study will elucidate the environmental correlates of ecosystem decline. However, even a cursory inspection of Appendixes A and B reveals that the most endangered ecosystems are typically at low elevations and have fertile soils, amiable climates, easy terrains, abundant natural resources, and other factors that encourage human settlement and exploitation. Exceptions include the high-elevation spruce-fir forests of the southern Appalachian Mountains that are affected by an exotic insect and air pollution (Pyne and Durham 1993) and the vast sagebrush steppe of the Intermountain West that is in many areas overgrazed by cattle (West, in press). Regional studies of ecosystem status should address the many potential causes of biotic impoverishment to devise effective conservation and restoration strategies.

The habitats that are most commonly recognized by the public and by conservation agencies as threatened in the United States are wetlands. Public-education campaigns have been moderately successful in expanding the awareness of wetland values and the severity of losses. Our study revealed that such efforts are warranted and should continue with increased attention to the particular wetland communities that are most endangered. However, most statistics on wetland losses are too generalized to be useful for biodiversity conservation. The category wetlands is too broad for establishing preferential protection. Some types of wetlands--for example, cattail (*Typha* spp.) marshes (other than in parts of the country where alien species such as purple loosestrife [*Lythrum salicaria*] threaten the integrity of many cattail ecosystems)--remain common in most regions and are in little need of protection. Others, such as California vernal pools and Atlantic white-cedar (*Chamaecyparis thyoides*) swamps, have an extremely restricted distribution today.

Our study also revealed that wetlands are not the only ecosystems in need of help. Across all regions of the United States, the most severe losses of area and natural quality have been in low elevation terrestrial

ecosystems and in aquatic ecosystems such as lakes, streams, and coastal bays. Although terrestrial ecosystems dominate our lists (Appendixes A and B), our methodology was probably biased against recognition of aquatic habitat losses. As noted above, most aquatic ecosystem declines involve qualitative changes--from, for example, dams, diversions, and pollution--rather than blatant removal of habitat. Because the heritage programs employ plant ecologists but usually not aquatic biologists, their databases typically contain little information on aquatic communities. A review of losses of aquatic biodiversity at stock (genetic), species, assemblage, fauna, ecosystem, and landscape levels of organization demonstrated that severe impoverishment is nationwide (Hughes and Noss 1992).

The need for an expansion of ecosystem conservation beyond wetland regulations is well illustrated in the southeastern coastal plain. Here, the decline of the once-dominant upland vegetation--longleaf pine--dwarfs the loss of wetlands. Longleaf pine, which once covered more than 60% of the uplands of the region and 40% of the entire region, has declined by more than 98%, whereas wetlands regionwide have declined by only about 28% (Fig. 3; Noss 1989; Ware et al. 1993). A review of the status of ecosystems in the Southeast revealed that "of all our natural biotic communities, the longleaf pine type may be the hardest to find in anything approaching its original condition" (Boyce and Martin 1993:349).

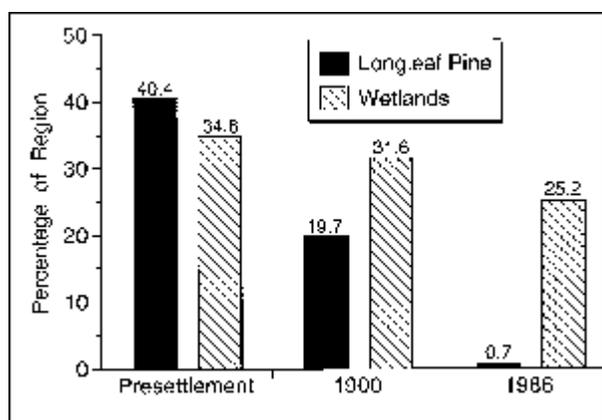


Fig. 3. Comparison of the percentage of southern mixed forest region (Kuchler 1966; essentially equivalent to southeastern coastal plain) that is composed of longleaf pine (*Pinus palustris*) and wetlands (all types) from Ware et al. (1993).

In Florida, which is famous for its wetlands, the most imperiled natural communities are uplands: 15 of 23 upland-community types are ranked S1 or S2 (critically imperiled or imperiled) by the Florida Natural Areas Inventory, whereas only 2 of 19 wetland communities are ranked this high (Noss and Wolfe 1990). Between 1936 and 1987, Florida lost 88% of its longleaf pine area but only 56% of its herbaceous wetlands (Kautz 1993). Since 1970, upland hardwood forests have declined by 27% and forested wetlands by 17%. Yet until recently, conservationists in the Southeast, as in other regions, have been most concerned about wetland losses. The federal Clean Water Act and state laws were enacted to protect wetlands but not uplands. Some rare upland communities in Florida have been destroyed by creating artificial wetlands to mitigate losses of natural wetlands (Hart 1987; Noss and Wolfe 1990). Mitigation has rarely been effective in conserving ecosystems of any type (Cabbage et al. 1993; Water Environment Federation 1993). A scientific and advocacy group in the Southeast--the Gopher Tortoise Council--concentrates on upland conservation issues, using the gopher tortoise (*Gopherus polyphemus*; a keystone species associated with longleaf pine and other threatened upland habitats) to promote the conservation of uplands (Noss and Wolfe 1990; Noss 1991a).

The great interest in wetlands by conservationists and agencies is most likely related to the widely recognized values of wetlands to human society: habitat for waterfowl and other game, nurseries for fishes, controllers of floods, cleansers of water, and many other services (Tiner 1984). In some regions, as in California and in the Midwest (Appendix B), losses of wetlands are among the most severe of any habitat. Rare species are often concentrated in wetlands, often because these systems are naturally rare or isolated in most regions, but also because so much wetland area has been destroyed (Tiner 1984). Although wetlands cover only about 5% of the land area of the United States, about 50% of the animals and 33% of the plant species listed in the United States as endangered or threatened in 1989 are dependent on wetlands (Nelson 1989). In Pennsylvania, 65% of 157 endangered plant species are associated with wetlands and 34% are wetland obligates. Of 510 species of

breeding vertebrates, 58% are considered wetland dependent; 82% of the threatened and endangered vertebrates are wetland dependent (Hassinger 1991).

In other regions, upland habitats or upland-wetland ecotones are where the greatest concentrations of rare and endangered species occur. A striking example is the enormous number of rare plants (191 taxa) and animals (at least 41 taxa in Florida) associated with longleaf pine and wiregrass (*Aristida stricta*) in the Southeast (Noss 1988; Hardin and White 1989). Of those species, 27 are federally listed as endangered or threatened and another 99 are proposed for listing by the U.S. Fish and Wildlife Service or are candidates for listing (Appendix E). The large number of rare plants and animals associated with longleaf pine or wiregrass is clearly related to the large geographic range of these two dominant species (longleaf pine in most of the southeastern and Gulf of Mexico coastal plains and wiregrass in the region west to Mississippi); the wide environmental gradient over which the rare plant and animal species occur (from xeric sandhills through seasonally wet savannas and herbaceous bogs); a geologic history that fostered evolution of narrow endemic taxa (Hardin and White 1989); and the staggering loss of these communities from agriculture, plantation forestry, and fire suppression.

As noted earlier, many losses of ecosystems have been associated with human settlement patterns. Habitats of all types--aquatic, wetlands, and uplands--have suffered more severe declines in coastal regions and in the vicinity of major rivers because these areas have been more intensively settled by people than other areas. Twenty-one (58%) of 36 federally listed threatened or endangered birds occur near coasts (not including species in Hawaii or Puerto Rico; E. T. LaRoe, unpublished data). Ecosystem protection is urgently needed in coastal zones.

Aquatic, wetland, and upland habitats are valuable to biodiversity and must be given protection that is commensurate with their endangerment. We suggest that education on wetlands and conservation of wetlands be expanded into ecosystem conservation. Endangered upland and aquatic ecosystems are likely to benefit if featured as prominently as endangered wetlands. Ideally, the scope of conservation should be enlarged to encompass the landscape, and thus avoid sometimes arbitrary and misleading divisions of continuous gradients into uplands and wetlands (Noss 1987).

Although we focus on declining and threatened ecosystems, some ecosystems in the United States are in relatively good condition or have recovered partially from past losses. Increases in forest cover during the last few decades have been noted in many regions, especially in the Northeast, in the upper Midwest, and in the South. Generally, conversion of forest to agriculture in the South peaked in the 1930's. During the past 50 years, croplands in Georgia declined by 50% and forest increased to 65% of total land use (Odum 1989). The greatest forest recovery has been in the Piedmont, where agricultural lands have declined by 60%; in contrast, little net change is apparent in the coastal plain (Turner and Ruscher 1988), except in Florida, where forest cover continues to decline (Kautz 1993).

Although the net increase in forest coverage in much of the South, Northeast, and upper Midwest and in some other regions is encouraging, the ecological qualities of second-growth and primary forests are dissimilar. Second-growth forests on former clear-cuts or in agricultural fields may take centuries to regain herbaceous floras and other qualities of old growth (Duffy and Meier 1992). Plantations (tree farms), now abundant in much of the country, are structurally and biologically less diverse than natural forests of any age and contain impoverished faunas (Means and Grow 1985; Noss 1989; Hansen et al. 1991; Sharitz et al. 1992). Humans can plant trees but cannot yet re-create a forest. Yet, plantations are often included in forest-cover statistics that forestry agencies cite in support of improving forest conditions (R. Noss, personal observation). This practice leads to misleading conclusions about forest conditions. The structure, function, and composition of any cover type must be assessed to assign biodiversity conservation value.

Correlation of Species Declines with Ecosystem Declines

The postulated function of a coarse filter (Master 1991a) is to save species by protecting samples of ecosystems. This hypothesis can be tested by determining whether declines of ecosystem types have been accompanied by

declines and extinctions of species that depend on or are associated with those ecosystems. Adequate data for tests are seldom available. Instead, historical evidence must be examined to discover the extent to which declines of populations are related to losses of particular habitats. A less powerful approach is to infer that rare species that are associated with endangered ecosystems, such as federally listed and candidate species (Appendixes C-E), became rare because the ecosystems on which they depend were degraded or reduced in area.

The Nature Conservancy estimated that perhaps 217 species of plants and 71 species and subspecies of vertebrates became extinct north of Mexico in North America and Hawaii since European settlement (Nature Conservancy 1992, Russell and Morse 1992). Of the presumably extinct plants, 95 were on the mainland and 122 were in Hawaii. Only three of the plant species were restricted to Canada. The list of extinct vertebrates is more certain than the plant list because many plants are considered possibly extinct because they have not been observed recently (R. Noss, personal observation). No reasonably complete list of extinct invertebrates is available, but we predict the number would be higher than that of plants because of the greater overall species richness and often restricted distributions of invertebrates. Undoubtedly, many invertebrates in the United States are still unknown to science.

The best documented causes of extinction are of vertebrates such as the great auk (*Pinguinus impennis*), Labrador duck (*Camptorhynchus labradorius*), heath hen (*Tympanuchus cupido cupido*), Carolina parakeet (*Conuropsis carolinensis*), passenger pigeon (*Ectopistes migratorius*), Steller's sea cow (*Hydrodamalis gigas*), and Caribbean monk seal (*Monachus tropicalis*). Multiple factors caused the demise of most of these species, but human hunting was primary. For example, the Carolina parakeet "clearly was exterminated by man; the birds were killed as agricultural pests, for food, and for sport. The bird was unusually susceptible to systematic killing; when a flock member was shot, its fellows would return again and again, so that a single hunter could take all the birds" (Hardy 1978:120). Until recently, overkill by humans was probably the major cause of animal extinctions, particularly marine mammals, large terrestrial mammals, and flightless birds, but has been replaced by habitat destruction in most regions (Diamond 1984). Hunting by Polynesians was responsible for the loss of some Hawaiian birds, especially large flightless species. However, most of the many extinct Hawaiian birds seem to have been lost from clearing lowland forests--especially dry leeward forests--for agriculture (Olson and James 1984).

Most lesser-known extinctions in the United States were probably caused by habitat loss. The list of extinct and possibly extinct plant species in the United States and Canada (Russell and Morse 1992) is dominated by narrow endemics, suggesting that the localized habitats of these species have been usurped by human activity. A recent review of federally listed threatened and endangered plant species in the United States (Cook and Dixon 1989) revealed that 81% are threatened by human activities, especially agriculture, mining, urban and suburban development, and exotic species. Similarly, a review of recovery plans for 98 plant species currently listed as threatened or endangered by the U.S. Fish and Wildlife Service revealed that habitat destruction by human activities was the primary cause of endangerment of 83% of the species (Schemske et al. 1994). Because many endemic plant species are concentrated in localized habitats, such as outcrops of rare rock types, coarse-filter protection of these habitats can be expected to save species more efficiently than a species-by-species approach. This may be true even where co-occurring species are rare for different reasons (Rabinowitz et al. 1986; Fiedler and Ahouse 1992).

The central role of habitat degradation in extinctions and declines of wetland and aquatic species is well established. More than 20% of the federally listed species in the United States may benefit from the protection of wetland habitats (Nelson 1989). Because more than 87% of recent wetland losses are attributable to agriculture (Nelson 1989), protecting wetland-associated species in many regions is largely a matter of reforming agricultural practices.

A review of factors that threaten biodiversity in rivers and streams revealed that habitat degradation of various kinds and introductions of nonindigenous species are the leading causes of species declines (Allan and Flecker 1993). Habitat degradation was a contributing factor in the extinction of at least 73% of the 27 species and 13

subspecies of freshwater fishes in North America during the last century (Miller et al. 1989). An earlier survey revealed that 81% of the nation's fish communities are adversely affected by anthropogenic factors; non-point source pollution was the most common cause (Judy et al. 1984). At least one-third of the freshwater fish taxa in North America is considered endangered, threatened, or of special concern by the American Fisheries Society; again, habitat loss and degradation are the major causes of endangerment (Williams et al. 1989). More specific regional studies revealed that habitat degradation (especially from water diversions for agriculture) and introduced nonindigenous species were primarily responsible for the decline of the native fish fauna in California (Moyle and Williams 1990) and that habitat destruction (e.g., from dams, logging, roads, and grazing) is the major cause of the decline of native salmonid stocks in the Northwest (Nehlsen et al. 1991). In contrast, human predation remains the greatest threat to many species in marine ecosystems. For example, the Northeast United States Shelf ecosystem, which encompasses 260,000 km² from the Gulf of Maine south to Cape Hatteras, has suffered major changes in fish-community structure during recent decades from overfishing of certain groups; pollution in this marine system has not been noticed except in small embayments (Sherman 1991).

Identification and protection of specific aquatic habitats and watersheds seem to be the most efficient means of safeguarding and restoring aquatic biodiversity because the number of species is too large for species-specific protection. Williams et al. (1989:18) called for ecosystem-level conservation to protect declining fish species:

"First, we encourage natural resource agencies to manage for conservation of entire ecosystems rather than recovery of individual species. Preservation of entire communities requires long-term commitments to habitat management, and results in more permanent protection than isolated recovery efforts."

Many other groups, including neotropical migrant birds (Terborgh 1989) and amphibians (Livermore 1992), are declining at the faunal level (multiple species) in many regions. Losses of amphibians are seemingly due to several factors, including habitat destruction, introductions of exotic predators and competitors, water pollution, and perhaps stratospheric ozone depletion (Livermore 1992; Blaustein 1993; Bury 1993). However, habitat destruction is probably the major cause of worldwide declines of amphibians (Blaustein 1993). The decline of neotropical migrant birds is even more closely linked to habitat destruction, particularly of forests, but is no less complex because forests are being lost and fragmented on the wintering grounds in the neotropics, on the breeding grounds in temperate regions, and in migration stopover habitat in between.

The dependence of many songbirds on large blocks of forest for successful breeding is well established (Whitcomb et al. 1981; Robbins et al. 1989a) despite problematic experimental designs of many studies (Haila et al. 1993). Recent (1978-87) declines of neotropical migrants evident from North American Breeding Bird Survey data suggest that declines are greatest among species that use neotropical forest habitats in winter (Robbins et al. 1989b). This information reflects the recent, increased severity of deforestation in the neotropics where many birds are concentrated in a smaller area than in North America. However, one analysis of the Breeding Bird Survey data revealed that nest predation and parasitism by cowbirds (*Molothrus* spp.) on the breeding grounds may be the most important factor in the decline of North American birds; species that are most susceptible to predation and parasitism have declined most (Bohning-Gaese et al. 1993). Conservationists should be concerned about habitat loss in all regions. As Robbins et al. (1989b:7661) pointed out:

"Habitat degradation in North America and the neotropics should not be viewed as alternative hypotheses for the population declines of neotropical migrants. Rather, evidence now supports the view that human activities in both regions are having dangerous impacts on the populations of migratory birds. Given the patterns of increasing forest destruction and fragmentation in both breeding and wintering areas of neotropical migrant birds, we predict that populations of migratory forest birds will continue to decline."

Ecosystem conservation that is oriented toward preserving small representative samples of various vegetation and habitat types--the familiar living-museum approach (Noss and Harris 1986)--does not address the problem of habitat fragmentation. Small, isolated samples of ecosystems will be depauperate from species-area effects, edge effects, and other problems associated with habitat fragmentation (Noss 1983; Harris 1984; Wilcove et al.

1986; Wilcove 1987; Noss and Csuti 1994). Preservation of species composition and integrity in these areas--even if they are rich in species at the time of establishment as reserves--cannot be expected. Successful ecosystem conservation must emphasize protection of large, interconnected landscapes (Noss 1983, 1992). In heavily fragmented regions, the sizes of reserves may be gradually enlarged by protecting and restoring adjacent lands. A long-term goal should be the reestablishment of natural connections between reserves. In all these cases, ecological restoration plans must be a primary component of conservation. Although restoration ecology is not yet a well developed science, degraded ecosystems should not be dismissed as lost causes.

We provided examples of how loss of habitat can lead to species declines. Such losses are not anecdotal or idiosyncratic; the pattern is obvious and examples are almost endless. But a reverse effect also occurs--species declines that cause ecosystem declines. The significant reduction of beavers (*Castor canadensis*) in North America from the early seventeenth to the twentieth century was partially responsible for the loss of wetlands during this period (Naiman et al. 1988). Because beavers create a complex successional mosaic of aquatic and terrestrial habitats across a landscape, they enrich landscape diversity and probably species diversity as well (Naiman et al. 1988). Although still trapped as nuisance animals in some areas, progressive land managers are using beavers to restore degraded streams and riparian zones (Naiman et al. 1988).

Similarly, pocket gophers (Geomyidae) have a tremendous influence on microtopography, soils, vegetation, and the biota of grasslands and other habitats. Plant communities with pocket gophers are usually more diverse than those without gophers (Huntly and Inouye 1988). The same can be said for prairie dogs (*Cynomys* spp.), which "modify and maintain large areas of the landscape that provide both refugia and propagule sources for plant species (e.g., early successional) that may only be able to disperse or become established under specific, but spatially and temporally unpredictable, circumstances" (Whicker and Detling 1988:780). Control of populations of these keystone animals has had significant effects on biodiversity at species and ecosystem levels. The consequences of reducing the great bison (*Bos bison*) thousand by 1890 (Zaveloff 1988) were largely undocumented, but the effects on grassland ecosystems were certainly profound (Reichman 1987). Domestic livestock is not an ecologically equivalent replacement (Plumb and Dodd 1993).

Some keystone species create unique structures that many other species use. Cavity-excavating birds, for example, provide roosting and nesting habitats for other birds, mammals, and invertebrates. If excavators decline, we predict that other species will also decline and have ripple effects through the ecosystem. Loss of gopher tortoises (*Gopherus polyphemus*) in the southeastern coastal plain--in part from poaching, but mostly from habitat destruction--may cause the decline or extirpation of dozens of species. Nearly 400 species of invertebrates and vertebrates have been found in gopher tortoise burrows, and some of them are obligate commensals (Jackson and Milstrey 1989). These findings suggest that ecosystem conservation should be designed to maintain optimal, not just minimally viable, populations of ecologically pivotal species in each ecosystem. Although loss of keystone species is a problem, addition of species (exotics) can also degrade ecosystems, such as the substantial degradation of the Everglades from the proliferation of the Australian tree *Melaleuca quinquenervia*. More generally, conservation should be integrated across levels of organization rather than be focused exclusively on genes, species, ecosystems, or any single level (Noss 1990).

Conclusions

The time is ripe for a concerted effort to identify and protect ecosystems across the United States, not only those that are presently endangered, but also those that are still in reasonably good condition. The public is becoming aware of the scientific fact that species coexist in functional systems. The public also has shown an increased interest in protecting and restoring entire ecosystems, not only single species. Wetland-protection initiatives, prairie restoration projects in the Midwest, ancient forest campaigns in the Pacific Northwest, and nationwide interest in forest protection are signs that the public cares about the condition of ecosystems. We believe our review of the literature and other sources demonstrates that the loss of biodiversity in the United States is occurring not only because of the extinction of individual species but because of the imperilment of entire ecosystems.

Ecosystem conservation is not a replacement for existing conservation measures such as the Endangered Species Act of 1973. Not all species that have gone extinct in the United States since European settlement would have been saved by a coarse filter, and a coarse filter does not protect all presently endangered species. When a species declines to where extinction is imminent, intensive efforts may be required for its recovery. But a strategy to represent all ecosystem types in areas managed for their natural values--keeping in mind the requirements of the most sensitive species--would be useful for keeping other species viable (Tear et al. 1993). It would almost certainly be more efficient and effective than the conventional species-by-species approach and would support the goal of maintaining overall biodiversity.

The question of how much area of each ecosystem or region must be protected from degradation to achieve conservation goals is beyond the scope of this paper, but estimates from biologists typically range from 25 to 75% (Odum 1970; Odum and Odum 1972; Margules et al. 1988; Noss 1991b, 1992; Noss and Cooperrider 1994). Maintaining or restoring this much of each region to natural habitat would not be technically, financially, or politically easy. However, in most cases, protected areas need not be entirely off-limits to human activities. Conservation biologists emphasize the need to develop land management that provides for biodiversity and direct human uses (Noss and Cooperrider 1994). Precisely what types of use are compatible with conservation objectives in any given case will always be a contentious issue, but is it not reasonable to propose that the burden of proof for compatibility fall on those who propose human activities in natural areas?

Many scientists and conservationists have noted the need for some kind of endangered-ecosystems legislation (Noss and Harris 1986; Hunt 1989; Orians 1993; M. Liverman, unpublished draft legislation), endangered-habitat act (Ehrlich and Ehrlich 1986), native-ecosystems act (Noss 1991a, 1991c; Noss and Cooperrider 1994), sustainable-ecosystems legislation (Jontz 1993), or other legislation that focuses on ecosystem protection. We do not discuss the relative merits of these proposals here, but some kind of proposed bill to the Congress seems inevitable soon. The bills that focused on ancient forests in the Pacific Northwest were essentially endangered-ecosystem bills applied on a regional scale and to a set of related ecosystems. The Natural Community Conservation Planning bill passed by the California legislature is also an example of ecosystem conservation. An advantage of the native-ecosystems concept (Noss 1991a, c) and of the sustainable-ecosystems idea of Jontz (1993) is that they are not restricted to ecosystems that have already suffered massive declines. Instead, like the philosophy behind the Gap-Analysis project (Scott et al. 1991a, 1991b, 1993), they seek proactively to sustain healthy samples of all native ecosystems nationwide. A similar goal was adopted by The Wildlands Project, a coalition of scientists and conservationists that hopes to restore a network of wild landscapes, replete with all native species, across North and Central America (Noss 1992).

Two major scientific projects that are currently underway will contribute to the conservation of ecosystems. One is a national classification of vegetation types by The Nature Conservancy and the Idaho Cooperative Fish and Wildlife Research Unit of the National Biological Service (Jennings 1993). A draft hierarchical classification to the series (dominant plant species) level in the western United States was produced (Bourgeron and Engelking 1992) and is consistent with a modified classification by the United Nations Educational, Scientific, and Cultural Organization (Driscoll et al. 1984). This framework is used to develop a national classification that allows consistent mapping of vegetation and other cover types across the United States by the gap-analysis project (Jennings 1993) and will presumably be used by The Nature Conservancy for ecosystem-level conservation (Grossman et al. 1994).

The second major work is the gap analysis itself, a nationwide assessment of the degree to which ecosystem types and species are represented in areas managed for their natural values (Scott et al. 1993). Identified gaps in the protection of species and ecosystems can be related to specific areas of land that, if protected, represent all elements in the most efficient manner (Scott et al. in preparation). This research is likely to provide a clearer picture of the status of ecosystems in the United States. However, these projects need to be supplemented by more specific studies of status and trends, for example, analyses of the extent of ecosystem decline, ecological consequences of loss and degradation, and current and potential threats to each ecosystem. Finally, conservation and restoration plans could be developed for each region and its component ecosystems.

Although our methods were not as rigorous as desirable because of the limitations of available data, the results provide the first reasonably comprehensive picture of endangered ecosystems in the United States and the first assessment of nationwide ecosystem decline since the study by Klopatek et al. (1979), which was based on 1967 data. When a national vegetation classification is completed, the types recognized in this report (Appendix A) can be cross-referenced to that system. However, as mentioned earlier, aquatic habitats, old-growth forests, virgin forests, grasslands not grazed by domestic livestock, and other qualitatively defined ecosystems of conservation significance are not encompassed by a classification system based strictly on vegetation or floristics. An assessment of the status of these important habitats will require a classification system with structural and other qualitative modifiers to the hierarchical classification.

A major recommendation from our study is that conservation plans for all ecosystems should be developed, starting with those that have suffered the most drastic declines (Appendix B) and that are at greatest risk of further losses or degradation. Protecting and restoring these ecosystems may avoid the need to list many of the species associated with them under the Endangered Species Act of 1973. When a suite of species associated with an ecosystem type qualifies for listing, these species can be listed together and restored to viability through multi-species conservation planning (Murphy et al. 1994). Such recovery plans exist for several assemblages of species (e.g., Bentzien 1987). This ecosystem-based approach to implementing the Endangered Species Act of 1973 is complementary to the listing and preparing of recovery plans for individual species. The immediate objective of protecting endangered ecosystems could be accomplished while working toward the longer-term and more difficult goals of representing all ecosystems adequately in protected areas, restoring degraded ecosystems to a natural and healthy condition, and managing ecosystems in reserves and multiple-use lands wisely.

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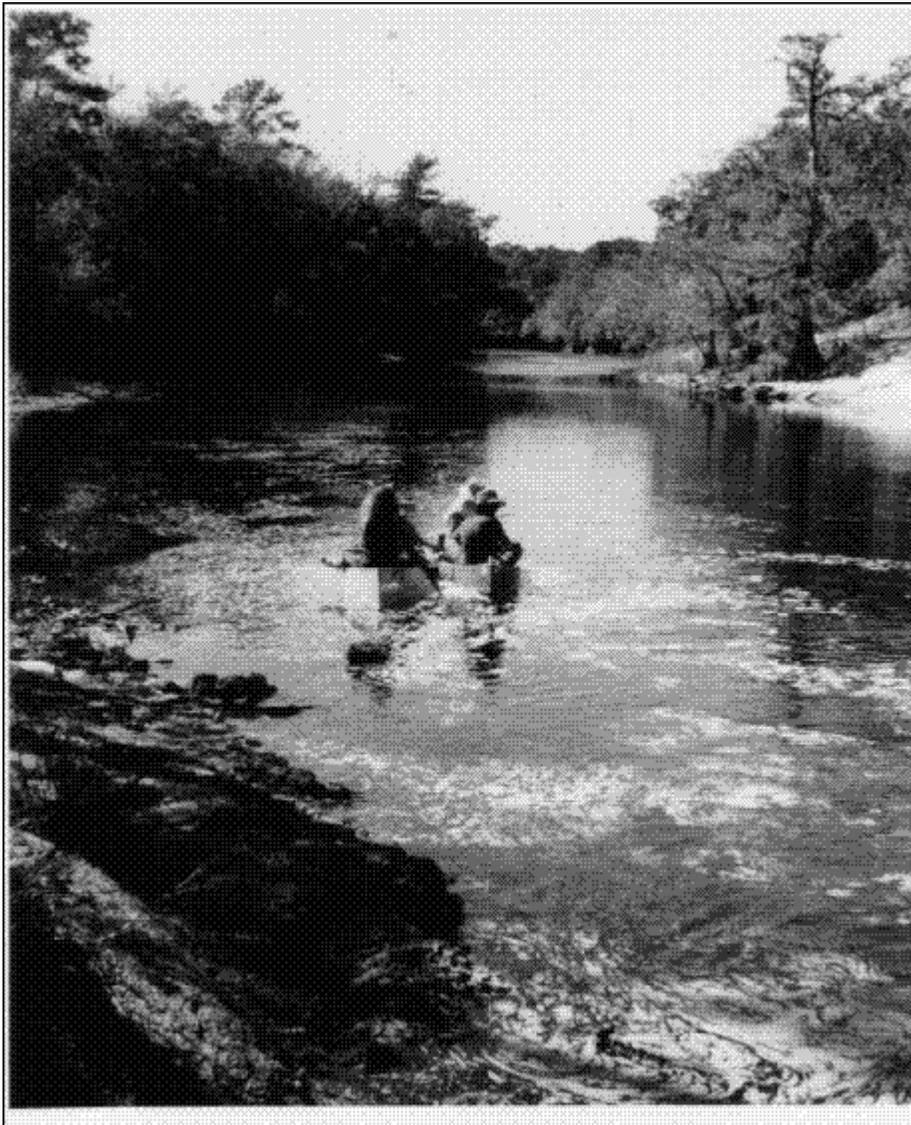
The red-cockaded woodpecker (*Picoides borealis*) candidate species that inhabit the endangered longleaf pine-wiregrass (*Pinus palustris-Aristida stricta*) ecosystem of the southeastern coastal plain. *Photo by R. Noss.*



View from the Apalachicola National Forest in Florida. Natural longleaf pine-wiregrass (*Pinus palustris-Aristida stricta*) savannas (*foreground*) have been converted to dense slash pine (*Pinus elliottii*) or loblolly pine (*Pinus taeda*) plantations (*background*)
Photo
by R. Noss.



A salt-marsh community. Many types of wetlands throughout the United States have experienced drastic reduction. Most information about the destruction of wetlands does not provide a distinction between imperiled wetland communities and other wetland types that remain common. *Photo by R. Noss.*



The Suwannee River in Florida. Natural, free-flowing rivers have become rare in the United States. About 98% of the streams in the United States are too degraded to be worthy of federal designation as wild or scenic rivers. The Suwannee River in Florida is one of the few major rivers that has remained without dams in the South. *Photo by R. Noss.*



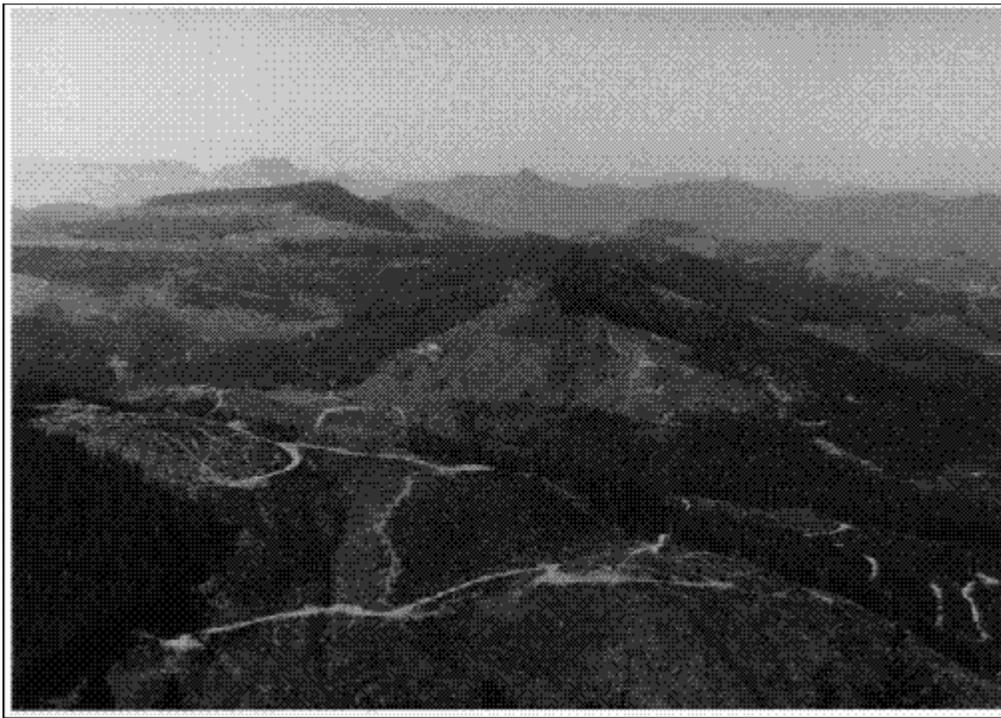
Ponderosa pine (*Pinus ponderosa*) ecosystems of the Intermountain West have become some of the most imperiled major forest types. Selective logging of the best trees and fire suppression have been responsible for most of the degradation. *Photo by R. Noss.*



Coastal sage scrub of southern California. About 70-90% of the presettlement coastal sage scrub in southern California has been destroyed mostly by residential development. Two federally listed species and 53 candidate species occur in this community. *Photo by R. Noss.*



Sagebrush (*Artemisia* spp.) steppe on the Malheur National Wildlife refuge in eastern Oregon. Although only about 10% of the sagebrush steppe that dominates the Intermountain West has been converted to anthropogenic habitats, more than 90% of this community is degraded by livestock grazing. *Photo by R. Noss.*



Old-growth forest in the Douglas-fir (*Pseudotsuga menziesii*) region of the Pacific Northwest. About 90% of this forest type has been destroyed by logging. The regional forest plan, proposed by President Clinton, would eliminate about 30% of remainder of this forest type. *Photo by R. Noss.*

Appendix A. Estimated declines of ecosystems with emphasis on the United States. Decline includes area loss and degradation (as noted). Estimates in each region generally proceed in the order of terrestrial vegetation and other terrestrial habitats, and wetland, aquatic, estuarine, and marine habitats.

50 United States

85% of original primary (virgin) forest destroyed by late 1980's (Postel and Ryan 1991).

90% loss of ancient (old-growth) forests (World Resources Institute 1992).

30% loss of wetlands from 1780's to 1980's (Dahl 1990).

12% loss of forested wetlands from 1940 to 1980 (Abernethy and Turner 1987).

81% of fish communities are adversely affected by anthropogenic limiting factors (Judy et al. 1984).

48 Conterminous States

ca. 95-98% of virgin forests destroyed by 1990 (estimated from map in Findley 1990 and commonly estimated by other authors, e.g., Postel and Ryan 1991).

99% loss of primary (virgin) eastern deciduous forest (Allen and Jackson 1992).

>70% loss of riparian forests since presettlement time (Brinson et al. 1981).

23% loss of riparian forest since the 1950's (Abernethy and Turner 1987).

53% loss of wetlands from 1780's to 1980's (Dahl 1990).

2.5% loss of wetlands between mid-1970's and mid-1980's (Dahl and Johnson 1991).

98% of an estimated 5.2 million km of streams are degraded enough to be unworthy of federal designation as wild or scenic rivers (Benke 1990).

Northeast

96% of virgin forests of northeastern and central states eliminated by 1920 (Reynolds and Pierson 1923).

88-90% loss of red spruce (*Picea rubens*) forest (spruce [*Abies* spp.]-fir [*Picea rubens*]) communities) in West Virginia (Boyce and Martin 1993; B. R. McDonald, West Virginia Division of Natural Resources, Elkins, W.Va., personal communication).

>90% of coastal heathland in southern New England and Long Island destroyed since mid-1800's (Godfrey and Alpert 1985).

>99.9% loss of Hempstead Plains grassland, Long Island, New York (Niering 1992; Reschke 1993).

10-50% loss of temperate eastern serpentine barrens (distributed from Georgia Piedmont to New York, but most in Pennsylvania and Maryland) and Pocono till barrens (Pennsylvania; R. Latham, University of Pennsylvania, Philadelphia, Pa., personal communication).

>98% probable loss of serpentine barrens, maritime heathland, and pitch pine (*Pinus rigida*) heath barrens in New York (interpretation from Reschke 1993).

>90% probable loss of the following terrestrial and wetland communities in New York: coastal plain Atlantic white-cedar (*Chamaecyparis thyoides*) swamp, maritime oak-holly forest (*Quercus* spp. <F128M>-<F255MI>Ilex spp.), maritime redcedar (*Juniperus virginianus*) forest, marl fen, marl pond shore, and oak openings (interpretation from Reschke 1993).

ca. 70-90% probable loss of the following terrestrial and wetland communities in New York: alvar grassland, calcareous pavement barrens, coastal plain poor fens, dwarf pine ridges, inland Atlantic white-cedar swamp, freshwater tidal swamp, inland salt marsh, mountain spruce-fir forest, patterned peatland, perched bog, pitch pine-blueberry peat swamp, rich graminoid fens, rich sloping fens, and riverside ice meadow (interpretation from Reschke 1993).

ca. 50% or less loss of the following in New York: Allegheny oak forest. Alpine krummholz, Great Lakes dunes, ice cave talus communities, perched swamp white oak swamp, rich shrub fen, and sandstone pavement barrens (interpretation from Reschke 1993).

60-68% loss of Long Island pine barrens (Cryan 1980).

37% loss of New Jersey pine barrens (Cryan 1985).

69% loss of pine barrens in Massachusetts (Cryan 1985).

48% loss of pine barrens across range (Connecticut, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island); >99% loss in some local areas of as many as 20,250 ha (Cryan 1985).

>97% loss to development of pine-oak-heath sandplain woods in the Lake Champlain basin of Vermont; remaining parcels degraded from fire suppression (R. Popp, Vermont Department of Fish and Wildlife, Nongame and Natural Heritage Program. Waterbury, Vt., personal communication). Almost total loss of lake sand beach in Vermont; only six degraded and fragmented examples are known to exist (R. Popp, Vermont Department of Fish and Wildlife, Nongame and Natural Heritage Program. Waterbury, Vt., personal communication).

>50% loss of pitch pine-scrub oak (*Pinus rigida-Quercus ilicifolia*) barrens in New Hampshire; one of two remaining large occurrences suffered >95% destruction (D. D. Sperduto, New Hampshire Department of Resources and Economic Development, Natural Heritage Inventory, Concord, N.H., personal communication).

100% loss (probably) of coastal rocky headland in New Hampshire (D. D. Sperduto, New Hampshire Department of Resources and Economic Development, Natural Heritage Inventory, Concord, N.H., personal communication), although this community is of questionable natural origin.

>99% loss of virgin or old-growth forests in New Hampshire (D. D. Sperduto, New Hampshire Department of Resources and Economic Development, Natural Heritage Inventory, Concord, N.H., personal communication).

>95% loss of floodplain forests in New Hampshire (D. D. Sperduto, New Hampshire Department of Resources and Economic Development, Natural Heritage Inventory, Concord, N.H., personal communication).

>50% loss or serious degradation of the following in New Hampshire: dry pitch pine-red pine (*Pinus rigida-Pinus resinosa* *Quercus* spp.-*Carya* spp.) forest, alpine/subalpine rocky summit, dry sandy riverbluff, inland beach strand, inland dune, coastal beach strand, coastal dune, inter-dunal swale, maritime forest on dunes, coastal plain pondshores (inland basin marsh and sandy pondshores), Atlantic white-cedar swamp, black gum-red maple (*Nyssa sylvatica-Acer rubrum*) basin swamp, calcareous fen, calcareous/circumneutral seepage swamp, fresh/brackish intertidal flat, moderately alkaline pond (D. D. Sperduto, New Hampshire Department of Resources and Economic Development, Natural Heritage Inventory, Concord, N.H., personal communication)

>30-50% loss of riverine bedrock barrens and sinkhole ponds in Maryland (L. Davidson, Maryland Department of Natural Resources, Natural Heritage Program, Annapolis, Md., personal communication).

>90% loss of low-elevation mesic limestone forest in Maryland (L. Davidson, Maryland Department of Natural Resources, Natural Heritage Program, Annapolis, Md., personal communication).

>95% loss of natural barrier island beaches in Maryland; >50% loss of barrier island dunes (L. Davidson, Maryland Department of Natural Resources, Natural Heritage Program, Annapolis, Md., personal communication). Almost total loss of bottomland hardwood forests in Ohio, lower Kanawha, and lower Monongahela River valleys in West Virginia (B. R. McDonald, West Virginia Division of Natural Resources, Elkins, W.Va., personal communication).

74% loss of wetlands in Connecticut between 1780's and 1980's (Dahl 1990).

97% of Connecticut's coastline developed (Olson 1984).

>50% of Connecticut's tidal wetlands lost since 1914 (Olson 1988).

54% loss of wetlands in Delaware between 1780's and 1980's (Dahl 1990).

20% loss of wetlands in Maine between 1780's and 1980's (Dahl 1990).

73% loss of wetlands in Maryland between 1780's and 1980's (Dahl 1990).

28% loss of wetlands in Massachusetts between 1780's and 1980's (Dahl 1990).

42% loss of wetlands in Massachusetts by 1988 (Massachusetts Executive Office of Environmental Affairs 1990).

9% loss of wetlands in New Hampshire between 1780's and 1980's (Dahl 1990).

39% loss of wetlands in New Jersey between 1780's and 1980's (Dahl 1990).

60% loss of wetlands in New York between 1780's and 1980's (Dahl 1990).

56% loss of wetlands in Pennsylvania between 1780's and 1980's (Tiner 1989; Dahl 1990; Hassinger 1991).

37% loss of wetlands in Rhode Island between 1780's and 1980's (Dahl 1990).

35% loss of wetlands in Vermont between 1780's and 1980's (Dahl 1990).

24% loss of wetlands in West Virginia between 1780's and 1980's (Dahl 1990).

Nearly total loss of free-flowing rivers in West Virginia; of major streams, only the Greenbrier River remains without dams (B. R. McDonald, West Virginia Division of Natural Resources, Elkins, W.Va., personal communication).

5.5% of surface waters in Massachusetts acidified in 1988 (Massachusetts Executive Office of Environmental Affairs 1990).

28.5% of lakes and ponds in Massachusetts threatened or impaired on the basis of eutrophic status in 1988 (Massachusetts Executive Office of Environmental Affairs 1990).

>50% loss of Delmarva bays (coastal plain seasonal ponds) in Maryland (L. Davidson, Maryland Department of Natural Resources, Natural Heritage Program, Annapolis, Md., personal communication).

>50-70% loss of coastal-plain ponds and pond shores in New York (interpretation from Reschke 1993).

20% of 23,833 miles (38,347 km) of assessed streams in Pennsylvania degraded from resource extraction (54.2%), agriculture (13.3%), and municipal point sources (9.2%; Frey 1990; Hassinger 1991).

61.5% of monitored estuaries and 26% of monitored rivers in Massachusetts affected by toxic chemicals in 1988 (Massachusetts Executive Office of Environmental Affairs 1990).

ca. 50-70% loss of the following aquatic and estuarine communities in New York: brackish intertidal mudflats, brackish intertidal shores, coastal plain streams (interpretation from Reschke 1993).

90% loss (from 250,000 to 25,000 ha) of submersed aquatic vegetation (seagrasses and freshwater angiosperms) in the Chesapeake Bay (Stevenson and Confer 1978; Orth et al. 1991).

South

100% loss of intact bluegrass savanna-woodland in Kentucky (T. Bloom, Kentucky Nature Preserves

Commission, Frankfort, Ky., personal communication).

>99.99% loss of native prairies in Kentucky (from 1.05 million to <<81 ha; Mengel 1965; Kentucky Environmental Quality Commission 1992).

99.999% loss (from 202,500 to 202 ha) of tallgrass prairie in Grand Prairie area of Mississippi Alluvial Plain in Arkansas (T. Foti, Arkansas Natural Heritage Inventory, Little Rock, Ark., personal communication).

Loss of all but a few small remnants of Black Belt Prairie in Alabama and Mississippi and Jackson Prairie in Mississippi to agriculture (DeSelm and Murdock 1993).

Loss of virtually all of the dry prairies of Florida to cattle pasture and agriculture (DeSelm and Murdock 1993).

>99.9% loss of prairie in Texas (Chapman 1993).

>99% loss of wet and mesic coastal prairies in Louisiana (Smith 1993).

95-99% loss of Mississippi terrace prairie in Louisiana (Smith 1993).

90-95% loss of calcareous prairies (all types) and Fleming glades in Louisiana; 75-90% loss of saline prairie (Smith 1993).

25-50% loss of coastal dune grassland, Catahoula sandstone glades, and coastal dune shrub thicket in Louisiana (Smith 1993).

>98% of presettlement longleaf pine (*Pinus palustris*) (Noss 1989; Ware et al. 1993).

97% loss of all natural upland vegetation types in the original range of longleaf pine; natural stands of longleaf pine reduced by about 99% (Frost in press).

95-99% loss of wet longleaf pine savannas and eastern upland longleaf pine forest in Louisiana; 75-90% loss of western upland longleaf pine forest (Smith 1993).

85% loss of natural longleaf pine forests in Texas and Louisiana since 1935 (Bridges and Orzell 1989).

Almost all of the loblolly-shortleaf pine (*Pinus taeda*-*Pinus echinata*)-hardwood forest of the West Gulf Coastal Plain (3.2 million ha) destroyed, mainly for conversion to loblolly pine plantations (T. Foti, Arkansas Natural Heritage Inventory, Little Rock, Ark., personal communication).

15% conversion of barrier island habitats (all types) on Atlantic and Gulf coasts to urban area by 1975; 300% increase in urban development from 1945 to 1975 (Lins 1980).

27% loss of total forest area in Florida from 1940 to 1980 (Knight and Mclure 1982).

88% loss of longleaf pine forests in Florida from 1936 to 1987 (Kautz 1993).

74.4% of xeric habitats (scrub, scrubby flatwoods, and sandhills) on southern Lake Wales ridge, Florida, lost to development or degraded (Peroni and Abrahamson 1985).

64% loss of Florida sand pine (*Pinus clausa*) scrub on Lake Wales, Lake Henry, and Winter Haven ridges since settlement (Christman 1988).

60.5% of flatwoods-swale habitats on southern Lake Wales Ridge, Florida, lost to development or degraded (Peroni and Abrahamson 1985).

88% loss of slash pine (*Pinus elliottii*) forests in southwestern Florida from 1900 to 1989 (Mazzotti et al. 1992).

>98% loss of pine rockland habitat (southern Florida; Bentzien 1987).

60-80% loss of tropical hardwood hammock on the central Florida keys (U.S. Fish and Wildlife Service 1985).

>99.98% loss of virgin forest in Kentucky; remaining stands are disturbed by factors such as grazing or chestnut blight (*Endothia parasitica*); current forest area is 54% of original (Mengel 1965; Kentucky Environmental Quality Commission 1992; T. Bloom, Kentucky Nature Preserves Commission, Frankfort, Ky., personal communication).

>80% of the original forests in the northern Georgia Piedmont cleared by 1930 (Bond and Spillers 1935).

ca. 95% loss of old-growth forests in the Cumberland Plateau of Tennessee and 80-90% loss in the Blue Ridge province of Tennessee (Pyne and Durham 1993).

35-57% loss of spruce-fir forest in the southern Appalachians, compared with 88% loss in West Virginia (Boyce and Martin 1993).

100% of spruce-fir forest in Tennessee was severely degraded from balsam wooly adelgid (*Adelges piceae*) infestation and probable air pollution effects, although only 10-20% of the habitat area has been lost; Pyne and Durham 1993).

50-60% conversion of Appalachian cove hardwood forests in the Blue Ridge province of Tennessee to non-forest habitats (Pyne and Durham 1993).

60-70% conversion of mixed mesophytic forest in the Cumberland Plateau of Tennessee to non-forest uses (Pyne and Durham 1993).

ca. 60% loss of oak-hickory forests on the Cumberland Plateau and Highland Rim of Tennessee; of the remaining 40%, <<5% is of high quality (Pyne and Durham 1993).

>90% loss of upland hardwoods in the coastal plain of Tennessee; only one high-quality example remains (Pyne and Durham 1993).

90% loss of ecologically intact limestone cedar (*Juniperus virginianus*) glades in Tennessee and ca. 50% loss of total cedar glade area (Pyne and Durham 1993).

95-99% loss of live oak (*Quercus virginiana*) oak-hackberry (*Quercus* spp. <F128M>-<F255MI>Celtis spp.) forest, and mature natural forests of all types combined in Louisiana (Smith 1993).

90-95% loss of shortleaf pine/oak-hickory forest, mixed hardwood loblolly pine forest, eastern xeric sandhill woodland, and stream terrace sandy woodland/savanna in Louisiana (Smith 1993).

75-90% loss of live oak-pine (*Pinus* spp.)-magnolia (*Magnolia* spp.) forest, mesic spruce pine ((*P. glabra*)-hardwood flatwoods, western xeric sandhill woodlands in Louisiana (Smith 1993).

50-75% loss of southern mesophytic forest, calcareous forest, hardwood slope forest in Louisiana; 50% loss of cedar woodlands (Smith 1993).

89% of 1.4 million ha of virgin forest in the Big Thicket, Texas, lost by 1960's (Parvin 1989).

78% decline of presettlement bottomland hardwood forests in the Southeast (Harris 1984).

56% of southern bottomland hardwood and baldcypress (*Taxodium distichum*.) forests lost between 1900 and 1978 (Bass 1989).

80% decline of presettlement bottomland hardwood forests in the lower Mississippi River Valley (Mississippi Alluvial Plain; MacDonald et al. 1979; Anderson 1991).

55% decline of bottomland hardwood forests in the lower Mississippi River alluvial floodplain from 1937 to 1978 (MacDonald et al. 1979).

82% loss of bottomland hardwood forests of eastern Oklahoma (Brabander et al. 1985).

60% loss of bottomland hardwood forests in Tennessee; remaining high quality stands are mostly on wetter sites (Pyne and Durham 1993) .

60-75% loss of baldcypress-tupelo (*Taxodium distichum*-*Nyssa* spp.) forest in the coastal plain and in the Mississippi alluvial plain of Tennessee (Pyne and Durham 1993).

85% of the forested wetlands of the Tensas Basin, Louisiana, cleared since 1937 (Gosselink et al. 1990).

75-90% loss of flatwood ponds, slash pine (*Pinus elliottii*)-pond cypress (*Taxodium ascendens*)/hardwood forest, wet mixed hardwood-loblolly pine (*Pinus taeda*) Louisiana (Smith 1993).

50-75% loss of freshwater marsh, interior saline soil marsh, scrub/shrub swamp, baldcypress/baldcypress-tupelo swamp, bottomland hardwood forest, bayhead swamp, and small-stream forest in Louisiana; 25-50% loss of hillside seepage bog, interior salt flat, gum swamp, seepage slope shrub thicket, and upland depressional swamp (Smith 1993).

95% loss of native habitat in lower delta of Rio Grande River, Texas; remains are highly fragmented (Riskind et al. 1987). Almost all large *Arundinaria gigantea* canebrakes lost; remaining cane exists mostly as an understory plant in forests or thickets along fencelines (Platt and Brantley 1992).

80-90% loss of upland wetlands in the Highland Rim of Tennessee (Pyne and Durham 1993).

>90% loss of Appalachian bogs in the Blue Ridge province of Tennessee (Pyne and Durham 1993).

90% loss of mountain bogs (Southern Appalachian bogs and swamp forest-bog complex, from 2,025 to 203 ha) in North Carolina (M. P. Schafale, North Carolina Department of Environment, Health, and Natural Resources, Division of Parks and Recreation, Natural Heritage Program, Raleigh, N.C., personal communication).

69% loss of pocosins (evergreen shrub bogs) in the southeastern coastal plain by 1980 (Richardson 1983).

69% loss of pocosins in North Carolina between 1952 and 1979 (33% converted to non-wetland uses; another 36% drained, cleared, or cut; Reffalt 1985).

>90% loss of pocosins in Virginia (T. J. Rawinski, Virginia Department of conservation and Recreation, Division of Natural Heritage, Richmond, Va., personal communication).

95% loss of ultramafic soligenous wetlands in The Glades region of Virginia (T. J. Rawinski, Virginia Department of conservation and Recreation, Division of Natural Heritage, Richmond, Va., personal communication).

98-99% loss of Atlantic white-cedar stands in the Great Dismal Swamp of Virginia and in North Carolina and probably across its entire range (Frost 1987; C. Frost, The Nature Conservancy, Minnesota Field Office, Minneapolis, Minn., personal communication).

28% of presettlement wetlands (all types combined) in the southeastern coastal plain lost by 1986 (Ware et al. 1993).

50% loss of wetlands in Alabama between 1780's and 1980's (Dahl 1990).

72% loss of wetlands in Arkansas between 1780's and 1980's (Dahl 1990).

46% loss of wetlands in Florida between 1780's and 1980's (Dahl 1990).

>50% loss of presettlement wetlands (all types) in Florida (Ewel 1988).

92% loss of mangrove swamp and salt marsh along Indian River Lagoon (Brevard, Indian River, and St. Lucie counties) between 1955 and 1974 from impoundment for mosquito control (Gilmore and Snedaker 1993).

56% decline of marsh (herbaceous wetland) habitat in Florida from 1936 to 1987 (Kautz in press).

51% loss of freshwater marshes in southwest Florida from 1900 to 1989 (Mazzotti et al. 1992).

25% of bayhead wetlands on the southern Lake Wales Ridge, Florida, lost to development or degraded (Peroni and Abrahamson 1985).

23% loss of wetlands in Georgia between 1780's and 1980's (Dahl 1990).

81% loss of wetlands in Kentucky between 1780's and 1980's (Dahl 1990).

79% loss of wetlands in Kentucky (59% drained for cropland, 20% converted to pasture; Kentucky Soil and Water Conservation Commission 1982).

46% loss of wetlands in Louisiana between 1780's and 1980's (Dahl 1990).

59% loss of wetlands in Mississippi between 1780's and 1980's (Dahl 1990).

49% loss of wetlands in North Carolina between 1780's and 1980's (Dahl 1990).

67% loss of wetlands in Oklahoma between 1780's and 1980's (Dahl 1990).

27% loss of wetlands in South Carolina between 1780's and 1980's (Dahl 1990).

59% loss of wetlands in Tennessee between 1780's and 1980's (Dahl 1990).

52% loss of wetlands in Texas between 1780's and 1980's (Dahl 1990).

42% loss of wetlands in Virginia between 1780's and 1980's (Dahl 1990).

>97% loss of Gulf Coast pitcher plant (*Sarracenia* spp.) bogs (Folkerts 1982).

Almost every stream in the Mississippi Alluvial Plain is channelized, leveed, or otherwise hydrologically altered (T. Foti, Arkansas Natural Heritage Inventory, Little Rock, Ark., personal communication).

>90% loss of aquatic mussel beds in Tennessee, mostly from impoundment but continuing declines from changes in water chemistry (Pyne and Durham 1993).

25-50% loss of most estuarine communities (salt marsh, brackish marsh, intermediate marsh, intertidal salt flat) in Louisiana; <<25% loss of vegetated pioneer emerging delta (Smith 1993).

ca. 50% alteration of mainland shoreline of Mississippi by seawall construction and artificial beach nourishment (Meyer-Arendt 1991).

33% loss of seagrass beds that existed in Florida before World War II (Holtz 1986a).

75% loss of seagrass meadows in Tampa Bay, Florida (Lewis 1992).

93% loss of seagrass meadows in Galveston Bay, Texas (Lewis 1992).

Midwest and Great Plains

90% of original 58 million ha of tallgrass prairie destroyed; remaining 10% mostly in small fragments (Madson 1990).

99% loss of tallgrass prairie east of the Missouri River; 85% loss west of the Missouri River (Klopatek et al. 1979; Chapman 1993).

>99.9% loss of tallgrass prairie in Iowa; remnants (ca. 12,150 ha) are mostly on dry and dry-mesic sites too rocky, sandy, dry, or inaccessible to plow (Smith 1981; J. A. Pearson, Iowa Department of Natural Resources, Des Moines, Iowa, personal communication).

99% to >99.9% loss of original tallgrass prairie in Illinois (The Nature Conservancy 1988, 1989a; Stolzenburg 1992; Chapman 1993).

>99% loss of original tallgrass prairie in Indiana (Chapman 1993).

Almost all black silt-loam and gravel hill tallgrass prairies of Indiana destroyed (Betz 1978).

99.5-99.7% loss of prairies in Ohio since settlement (Cusick and Troutman 1978; P. D. Jones, Ohio Department of Natural Resources, Columbus, Ohio, personal communication).

99.93% loss of original blacksoil prairie in Michigan (Chapman 1984; D. Albert, Michigan Natural Features Inventory, Lansing, Mich., personal communication).

99.3% loss of original dry sand prairie in Michigan (Chapman 1984; Albert 1992).

ca. 99.5% loss of lakeplain wet prairie in Michigan; only 203 ha persist (Chapman 1984; Albert 1992).

99.5% loss of original 6.1 million ha of tallgrass prairie in Missouri (Schroeder 1982; Toney 1991; T. A. Nigh, Missouri Department of Conservation, Jefferson City, Mo., personal communication).

>97% loss of tallgrass prairie that once covered the eastern one-third of Nebraska (Chapman 1984; G. Steinauer 1992; Nebraska Games and Parks Commission, Lincoln, Nebr., personal communication).

ca. 5% loss of sandhills prairie covering north-central Nebraska (Steinauer 1992).

ca. 82% loss of tallgrass prairie in Kansas (Chapman 1984).

>99% loss of original tallgrass prairie in Minnesota; probably more than half of remainder is in tracts of <40 ha, more than 75% is in tracts <260 ha, few tracts of >400 ha, and none is >1000 ha (R. Dana, Minnesota Department of Natural Resources, St. Paul, Minn., personal communication).

ca. 47% loss of native grassland in South Dakota by 1977; significant but undocumented losses since then; bluestem prairie declined by about 85% and wheatgrass-bluestem-needlegrass (*Agropyron-Andropogon-Stipa* spp.) prairie by about 70% (D. Backlund, South Dakota Department of Fish, Game, and Parks, Pierre, S.Dak., personal communication).

90% loss of native grassland in North Dakota (Madson 1989).

35% loss of forest since settlement in Iowa (Thomson and Hertel 1981); however, most of this loss was probably savanna (Thomson 1987), which is almost extinct (J. A. Pearson, Iowa Department of Natural Resources, Des Moines, Iowa, personal communication).

99.98% of oak savanna in the Midwest eliminated between settlement and 1985; less than 0.004% of

>99% loss of original oak barrens (dry savanna) in Michigan, but about 2% remains in good to restorable condition; no known intact examples of oak openings (mesic and dry-mesic savanna; Albert 1992).

99.98% of oak savanna in Missouri destroyed or degraded by fire suppression (Nelson 1985); an undetermined area of degraded savanna is restorable (T. A. Nigh, Missouri Department of Conservation, Jefferson City, Mo., personal communication).

99.98% of oak savanna in Minnesota destroyed; remaining 500 ha all on wind-modified outwash or fluvial sands (Nuzzo 1986; R. Dana, Minnesota Department of Natural Resources, St. Paul, Minn., personal communication).

ca. 78% of aspen (*Populus tremuloides*) parkland in Minnesota destroyed (Nuzzo 1986; R. Dana, Minnesota Department of Natural Resources, St. Paul, Minn., personal communication).

70% of presettlement jack pine (*Pinus banksiana*

86% loss of red (*Pinus resinosa*) and white pine (*Pinus strobus*) forest area in Minnesota (Frehlich et al. 1992), and much of remainder is in red pine plantations (K. A. Rusterholz, Minnesota Department of Natural Resources, St. Paul, Minn., personal communication). Boreal hardwood-conifer forest in Minnesota increased by 26% (Frehlich et al. 1992), but much of that area is in white spruce (*Picea glauca*) plantations (K. A. Rusterholz, Minnesota Department of Natural Resources, St. Paul, Minn., personal communication).

72% loss of northern hardwood forest in Minnesota (Frehlich et al. 1992).

57% loss of swamp conifer forestland in Minnesota (Frehlich et al. 1992).

14% loss of riverbottom forest in Minnesota (Frehlich et al. 1992).

99.95% loss of high-quality, mature to old-growth white pine-red pine forest in Michigan (Albert 1992).

99.92% loss of mature to old-growth oak forest (mesic to dry, without pine) in Michigan (Albert 1992).

99.95% loss of mature to old-growth mesic beech-maple (*Fagus grandifolia*-*Acer saccharum*) forest in Michigan (Albert 1992).

>99.9% loss of old-growth forest in the central hardwood region (Parker 1989).

95.9% of lowland forest in southeastern Missouri destroyed (Korte and Frederickson 1977); more has been lost since 1977 (T. A. Nigh, Missouri Department of Conservation, Jefferson City, Mo., personal communication).

>85% loss of original forest area in Ohio between settlement and 1939, followed by recovery to about 27% of total land area (28% of original area) by 1977; only a few small patches of old growth remain (Good 1979; King 1990; P. D. Jones, Ohio Department of Natural Resources, Columbus, Ohio, personal communication; personal observation).

55% loss of wetlands in the Great Lakes states (Council on Environmental Quality 1989).

89% loss of wetlands in Illinois (Reffalt 1985).

85% loss of wetlands in Illinois between 1780's and 1980's (Dahl 1990).

>99% of wetlands in Illinois destroyed (Holtz 1986b).

87% loss of wetlands in Indiana between 1780's and mid-1980's (Dahl 1990).

98.9% loss of presettlement wetlands in Iowa (from 2.3 million to 26,470 acres; Reffalt 1985).

89% loss of wetlands in Iowa between 1780's and 1980's (Dahl 1990).

40% of potential fen sites (and 65-77% of actual fens) in Iowa destroyed by cultivation or drainage; most of the remaining fens altered or threatened by grazing, cropland edge effects, woody plant invasion, drainage, excavation, or mining (Pearson and Leoschke 1992).

48% loss of wetlands in Kansas between 1780's and 1980's (Dahl 1990).

71% loss of wetlands in Michigan (Reffalt 1985).

50% loss of wetlands in Michigan between 1780's and 1980's (Dahl 1990).

80% loss of southern tamarack (*Larix laricina*) remain in southern lower Michigan (Albert 1992).

60-70% loss of coastal marsh in Michigan by 1980's; more developed since (Albert 1992).

46% loss of wetlands in Wisconsin from 1780's to 1980's (Dahl 1990).

>99% loss of original sedge meadows in Wisconsin (Reuter 1986).

50% loss of wetlands in Minnesota between 1780's and 1980's (Dahl 1990).

90% loss of wetlands in Missouri (Reffalt 1985).

87% loss of wetlands in Missouri between 1780's and 1980's (Dahl 1990); much of what remains is of low

quality with altered hydrology (T. A. Nigh, Missouri Department of Conservation, Jefferson City, Mo., personal communication).

35% loss of wetlands in Nebraska between 1780's and 1980's (Dahl 1990).

>90% of original wetlands and 78% of original wetland acres destroyed in Rainwater Basin of south-central Nebraska (Nebraska Game and Parks Commission 1972, 1974; Reffalt 1985).

ca. 90% loss of eastern Nebraska saline wetlands in Lancaster and Saunders counties (Farrar and Gersib 1991).

90% loss of wetlands in Ohio from 1780's to 1980's (Dahl 1990).

57% loss of forested wetlands in Ohio since 1940 (Birch and Wharton 1982).

25% of Ohio's fens destroyed (Stuckey and Denny 1981).

49% loss of wetlands in North Dakota from 1780's to 1980's (Dahl 1990).

35% loss of wetlands in South Dakota from 1780's to 1980's (Dahl 1990).

60% and 40% of the original wetland area drained in North Dakota and South Dakota, respectively (Tiner 1984; Kantrud et al. 1989).

60-65% loss of prairie potholes in upper Great Plains (Council on Environmental Quality 1989; Madson 1989).

Rocky Mountains

60-70% of old-growth ponderosa pine (*Pinus ponderosa*) more accessible areas are high-graded (logged of superior trees; B. Moseley, Idaho Conservation Data Center, Nongame and Endangered Wildlife Program, Boise, Idaho, personal communication).

ca. 70% loss of maritime-like forests in the Clearwater Basin of Idaho, much of remainder highly fragmented (B. Moseley, Idaho Conservation Data Center, Nongame and Endangered Wildlife Program, Boise, Idaho, personal communication)

80-90% loss of low elevation, high productivity, old-growth forests in western Montana (Chadde 1992).

80-90% loss of low-elevation native grasslands in western Montana (Chadde 1992).

50% loss of wetlands in Colorado between 1780's and 1980's (Dahl 1990).

56% loss of wetlands in Idaho between 1780's and 1980's (Dahl 1990); probably 80-90% of lower-elevation wetlands were lost and most of the rest was degraded (B. Moseley, Idaho conservation Data Center, Nongame and Endangered Wildlife Program, Boise, Idaho, personal communication).

27% loss of wetlands in Montana between 1780's and 1980's (Dahl 1990).

80-90% loss of woody hardwood draws in eastern Montana; glacial pothole ponds in the Mission and Swan valleys, on the Blackfeet Reservation, and in the northeastern prairie pothole region; and peatlands in Montana (Chadde 1992).

38% loss of wetlands in Wyoming between 1780's and 1980's (Dahl 1990).

95% of waters in Montana degraded or had losses of native species and invasion of exotics (D. L. Genter, Montana Natural Heritage Program, Helena, Mont., personal communication).

California

99% loss of native grassland (from 9 million to 89,100 ha; Kreissman 1991).

94.2% loss of native grassland in San Diego County (Oberbauer 1990).

26% of native annual and perennial grasslands destroyed between 1945 and 1980 (Mayer and Laudenslayer 1988).

8,653% increase in non-native annual grassland (Barbour et al. 1991).

99.9% loss of needlegrass steppe (Barbour et al. 1991).

90% loss of northern coastal bunchgrass (Barbour et al. 1991).

68.2% loss of alpine meadows (Barbour et al 1991).

100% loss of coastal strand in San Diego county (Oberbauer 1990).

70-90% of presettlement southern California coastal sage scrub destroyed (Westman 1981; Atwood 1990; Oberbauer 1990; O'Leary 1990; U.S. Fish and Wildlife Service 1992).

66% or less of southern California coastal sage scrub lost since settlement (Jones 1991).

91.6% loss of maritime sage scrub and 87.7% loss of coastal mixed chaparral in San Diego County (Oberbauer 1990).

>99% loss (virtual extirpation) of alkali sink scrub in southern California (Freas and Murphy 1988, D. D. Murphy, Center for Conservation Biology, Stanford University, Stanford, Calif., personal communication).

8.7% loss of chaparral and 81.3% increase in montane chaparral (Barbour et al. 1991).

25% of non-federal forests and rangelands are experiencing excessive surface soil erosion (U.S. Soil Conservation Service 1984).

85% loss of coastal redwood (*Sequoia sempervirens*) forests (Wilburn 1985).

32% loss of redwood forests and mixed conifer forests; 12% loss of Douglas-fir (*Pseudotsuga menziesii*) forests (Barbour et al. 1991).

72% loss of woodland and chaparral on Santa Catalina Island (O'Malley 1991).

14% loss of hardwood woodlands (Bolsinger 1988).

89% loss of riparian woodland statewide (Kreissman 1991).

88.9% loss of Central Valley riparian forests (Barbour et al. 1991).

99% of Central Valley riparian forests destroyed within 100 years after settlement (Reiner and Griggs 1989).

- 90-98% decline of Sacramento River riparian and bottomland forests (The Nature Conservancy 1990; Jacobs 1992).
- 99.9% loss of Central Valley riparian oak forest (Martin 1986).
- 60.8% loss of riparian woodland in San Diego County (Oberbauer 1990).
- 91% loss of wetlands (all types) between 1780's and 1980's (Dahl 1990).
- 94% loss of inland wetlands (Barbour et al. 1991).
- 69% loss of tule (*Scirpus*) marsh (Barbour et al. 1991).
- 94-96% loss of Central Valley interior wetlands (Reffalt 1985; Jensen et al. 1990; Kreissman 1991).
- 31.5% loss of wetlands and deepwater habitats in the Central Valley between 1939 and mid-1980's (Frayner et al. 1989).
- 66-88% loss of Central Valley vernal pools (Holland 1978; Kreissman 1991).
- 96.5% loss of vernal pools in San Diego County (Oberbauer 1990).
- 90.1% loss of freshwater marsh in San Diego County (Oberbauer 1990).
- 80% of coastal wetlands converted to urban or agricultural uses (Jensen et al. 1990; Barbour et al. 1991; Kreissman 1991).
- 62% loss of salt marshes (MacDonald 1977).
- 87.8% loss of coastal salt marsh in San Diego County (Oberbauer 1990).
- 90% loss of seasonal wetlands around the San Francisco Bay (Jensen et al. 1990).
- 80% loss of tidal marshes in the San Francisco Bay (Lewis 1992).

Southwest and Intermountain West

30% of 4.4 million km² of arid and semi-arid lands severely desertified and another 60% slightly desertified (Dregne 1983).

10% loss of sagebrush steppe to dryland or irrigated agriculture (West 1994).

>99% of remaining sagebrush steppe has been affected by livestock and about 30% has been heavily grazed, with dominance concentrated in a few woody plants (West 1994).

>99% of basin big sagebrush (*Artemisia tridentata tridentata*) in the Snake River plain of Idaho converted to agriculture (Hironaka et al. 1983; B. Moseley, Idaho Conservation Data Center, Nongame and Endangered Wildlife Program, Boise, Idaho, personal communication). 2-2.43 million ha of sagebrush-grass steppe in the western Snake River basin converted to exotic annual vegetation, primarily cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum asperum*), ultimately from overgrazing (Pellant 1990; Whisenant 1990; B. Moseley, Idaho Conservation Data Center, Nongame and Endangered Wildlife Program, Boise, Idaho, personal communication)

>90% loss of native shrub-steppe grassland in Oregon and in southwestern Washington (The Nature Conservancy 1992).

99.9% of Palouse prairie throughout its range in Idaho, Oregon, and Washington lost to agriculture; see also Washington regional summary below (Tisdale 1961; B. Moseley, Idaho Conservation Data Center, Nongame and Endangered Wildlife Program, Boise, Idaho, personal communication).

ca. 50% of current western juniper (*Juniperus occidentalis*) in Idaho is invasive, having replaced sagebrush-grass communities after fire suppression (Burkhardt and Tisdale 1969, 1976; B. Moseley, Idaho Conservation Data Center, Nongame and Endangered Wildlife Program, Boise, Idaho, personal communication). Almost all riverine cottonwood (*Populus* spp.) forests on big rivers of southern Idaho lack recruitment of younger age classes, mostly from dams eliminating spring flooding that exposed mineral soil needed for germination (B. Moseley, Idaho Conservation Data Center, Nongame and Endangered Wildlife Program, Boise, Idaho, personal communication).

83% of riparian area under management of the U.S. Bureau of Land Management in unsatisfactory condition and in need of restoration plans (Almand and Krohn 1979).

90% loss of presettlement riparian ecosystems in Arizona and in New Mexico (Arizona State Parks 1988).

36% loss of wetlands in Arizona between 1780's and 1980's (Dahl 1990).

70% loss of cienegas (wet marsh) sites in Arizona since settlement (Arizona Nature Conservancy 1987).

52% loss of wetlands in Nevada between 1780s and 1980's (Dahl 1990).

93.3% loss of marshes (from 31,995 to 21,465 ha) in the Carson-Truckee area of western Nevada (Reffalt 1985).

33% loss of wetlands in New Mexico between 1780's and 1980's (Dahl 1990).

30% loss of wetlands in Utah between 1780's and 1980's (Dahl 1990).

Pacific Northwest (Cascade Mountains and westward)

83-90% loss of old-growth forests in Douglas-fir region of Oregon and Washington (Harris 1984; Spies and Franklin 1988; Norse 1990).

96% of original coastal temperate rainforests in Oregon logged (Kellogg 1992).

75% of original coastal temperate rainforests in Washington logged (Kellogg 1992).

92-98% loss of old-growth ponderosa pine forests in three sample national forests (Deschutes, Fremont, and Winema) in Oregon (Eastside Forests Scientific Society Panel 1993).

28% of Washington's native vegetation destroyed (i.e., altered or covered soil profiles); the greatest losses were in the Palouse (74%), northern and southern Puget lowlands (51% and 49%, respectively), Yakima Folds (47%) and Scabland basins (47%) regions (R. C. Crawford, Washington Department of Natural Resources, Division of Land and Water Conservation, Natural Heritage Program, Olympia, Wash., personal communication).

99.5% loss of native grasslands and oak savannas in the Willamette Valley, Oregon, since European settlement (Ingersoll and Wilson 1991).

99.9% loss of native prairie (all types combined) in the Willamette Valley, Oregon, since European settlement (Alverson 1992).

38% loss of wetlands in Oregon between 1780's and 1980's (Dahl 1990).

85% loss of marshlands in the Coos Bay area of Oregon (Reffalt 1985).

70% loss of marshlands in the Puget Sound and 50% in the Willapa Bay areas of Washington (Reffalt 1985).

31% loss of wetlands in Washington between 1780's and 1980's (Dahl 1990).

33% loss of wetlands in Washington by 1980's; deepwater habitat decreased by only 4% (Canning and Stevens 1989).

Alaska

11% of original coastal temperate rainforests logged (Kellogg 1992).

0.1% loss of wetlands between 1780's and 1980's (Dahl 1990).

Hawaii

80% of original habitat below 458 m severely altered by the year 1800 (Holing 1987).

67% of original forest cover lost, including 50% of rain forests (Hawaii State Department of Land and Natural Resources et al. 1992).

90% loss of dry forests, shrubland, and grassland on all main islands combined (Hawaii State Department of Land and Natural Resources et al. 1992; Hawaii Heritage Program 1992).

61% loss of mesic forest and shrubland on all main islands combined (Hawaii State Department of Land and

42% loss of wet forest, shrubland, and bog on all main islands combined (Hawaii State Department of Land and

3% loss of subalpine forest, shrubland, and desert on all main islands combined (Hawaii State Department of Land and Natural Resources et al. 1992, Hawaii Heritage Program 1992).

74 (52%) of 141 natural-community types are considered imperiled or critically imperiled globally (Hawaii Heritage Program 1991).

12% loss of wetlands between 1780's and 1980's (Dahl 1990).

International Comparisons

Worldwide

76% of original primary forest worldwide destroyed by late 1980's (Postel and Ryan 1991 from various sources).

ca. 50% of original area of tropical forest worldwide destroyed (Postel and Ryan 1991 from various sources).

55% of original coastal temperate rainforest worldwide logged (Kellogg 1992).

North and Central America and Caribbean

41% of original coastal temperate rainforest in North America logged (Kellogg 1992).

48% of original primary forest destroyed in Canada by late 1980's (Postel and Ryan 1991 from various sources).

60% of old-growth forests in Canada lost to logging (World Resources Institute 1992).

57% of original coastal temperate rainforest in British Columbia logged (Kellogg 1992).

ca. 66% each of Atlantic salt marshes, prairie wetlands, and Pacific estuarine marshes in Canada destroyed (Ryan 1992).

>90% of southern Mexico's rainforest destroyed (Ross 1992).

45% of Mexico's remaining forest significantly disturbed (The Nature Conservancy 1986).

60% loss of primary forest in Guatemala (The Nature Conservancy 1989b).

98% loss of dry forest in western central America (Jordan 1987; McLarney 1989).

>99% of original forest in Puerto Rico destroyed by 1900, although coffee plantations covering 9% of island contained remnant individual dominant trees (Brash 1987; Weaver 1989).

75% loss of primary forest in Jamaica (The Nature Conservancy 1989c).

South America

37% of original primary forest destroyed in Brazil by late 1980's (Postel and Ryan 1991 from various sources).

10% of Brazilian Amazon forests destroyed (Ryan 1992).

98.5% of Brazilian Atlantic coastal forests destroyed (McNeely et al. 1990).

40% of original primary forest destroyed in Peru by late 1980's (Postel and Ryan 1991 from various sources).

29% of original primary forest destroyed in Venezuela by late 1980's (Postel and Ryan 1991 from various sources).

74% of original primary forest destroyed in Columbia by late 1980's (Postel and Ryan 1991 from various sources).

ca. 50% of mangroves cleared in Ecuador (Ryan 1992).

58% of original coastal temperate rainforests in Chile and Argentina logged (Kellogg 1992).

Africa and Madagascar

65% of original wildlife habitat lost in Africa south of the Sahara (IUN/UNEP 1986a).

44% of original primary forest destroyed in Zaire by late 1980's (Postel and Ryan 1991 from various sources).

70-80% of original forest, savannah, and wetlands in Nigeria destroyed (World Resources Institute 1992).

70% loss of mangrove forests in Mozambique over last 20 years (World Resources Institute 1992).

>90% of natural vegetation of Madagascar destroyed (Raven 1986).

75% loss of forests in Madagascar (World Resources Institute 1992).

Europe

>99% of original primary forest destroyed in Europe by late 1980's. (Postel and Ryan 1991 from various sources).

>99% of original coastal temperate rainforest logged (Kellogg 1992).

99.2% of the Caledonian forest of Scotland cleared (Watson 1992).

>96% of raised bogs in The Netherlands and Britain damaged (WRI, IUCN, UNEP 1992).

95% of original peatlands in Ireland modified (Breining 1992).

>50% of original peatlands in Finland drained (Breining 1992).

Asia

67% of original wildlife habitat lost in tropical Asia (IUCN/UNEP 1986b).

94% of original vegetation of Bangladesh destroyed (WRI, IUN, UNP 1992).

58% of original primary forest destroyed in Papua New Guinea by late 1980's (Postel and Ryan 1991 from various sources).

57% of original primary forest destroyed in Indonesia by late 1980's (Postel and Ryan 1991 from various sources).

>75% of mangrove forests destroyed in India, Pakistan, and Thailand (Ryan 1992).

99% of original primary forest destroyed in China by late 1980's (Postel and Ryan 1991 from various sources).

Australia and New Zealand

95% of original primary forest destroyed in Australia by late 1980's (Postel and Ryan 1991 from various sources).

15% of original coastal temperate rainforest in Australia logged (Kellogg 1992).

76% of original primary forest destroyed in New Zealand by late 1980's (Postel and Ryan 1991 from various sources).

72% of original coastal temperate rainforest in New Zealand logged (Kellogg 1992).

Appendix B. Critically endangered, endangered, and threatened ecosystems of the United States. Decline refers to destruction, conversion to other land uses, or significant degradation of ecological structure, function, or composition since European settlement. Estimates (see references in Appendix A) are from quantitative studies and qualitative assessments.

Critically Endangered (>98% decline) Ecosystems

Old-growth and other virgin stands in the eastern deciduous forest biome.

Spruce-fir (*Picea rubens*-*Abies fraseri*) forest in the southern Appalachians.

Red pine (*Pinus resinosa*) and white pine (*Pinus strobus*) forests (mature and old-growth) in Michigan.

Longleaf pine (*Pinus palustris*)

Slash pine (*Pinus elliottii*) rockland habitat in South Florida.

Loblolly pine-shortleaf pine (*Pinus taeda*-*Pinus echinata*) hardwood forests in the West Gulf Coastal Plain.

Arundinaria gigantea canebrakes in the Southeast.

Tallgrass prairie east of the Missouri River and on mesic sites across range.

Bluegrass savanna-woodland and prairies in Kentucky.

Black Belt prairies in Alabama and Mississippi and in the Jackson Prairie in Mississippi.

Ungrazed dry prairie in Florida.

Oak (*Quercus* spp.) savanna in the Midwest.

Wet and mesic coastal prairies in Louisiana.

Lakeplain wet prairie in Michigan.

Sedge (*Carex* spp. and others) meadows in Wisconsin.

Hempstead Plains grasslands on Long Island, New York.

Lake sand beaches in Vermont.

Serpentine barrens, maritime heathland, and pitch pine (*Pinus rigida*)-heath barrens in New York.

Prairies (all types) and oak savannas in the Willamette Valley and in the foothills of the Coast Range, Oregon.

Palouse prairie (Idaho, Oregon, and Washington and in similar communities in Montana).

Native grasslands (all types) in California.

Alkali sink scrub in southern California.

Coastal strand in southern California.

Ungrazed sagebrush steppe in the Intermountain West.

Basin big sagebrush (*Artemisia tridentata*) in the Snake River Plain of Idaho.

Atlantic white-cedar (*Chamaecyparis thyoides*)
Carolina and possibly across the entire range.

Streams in the Mississippi Alluvial Plain.

Endangered (85-98% decline)

Old-growth and other virgin forests in regions and in states other than in those already listed, except in Alaska.

Mesic limestone forest and barrier island beaches in Maryland.

Quercus spp.-*Ilex* spp.) forest, maritime
redcedar (*Juniperus virginiana*) forest, marl fen, marl pond shore, and oak openings in New York.

Pine-oak-heath sandplain woods and lake sand beach in Vermont.

Floodplain forests in New Hampshire.

Red spruce (*Picea rubens*) forests in the central Appalachians (West Virginia).

Upland hardwoods in the Coastal Plain of Tennessee.

Lowland forest in southeastern Missouri.

High-quality oak-hickory (*Quercus* spp.-*Carya* spp.) forest on the Cumberland Plateau and on the Highland Rim of Tennessee.

Limestone redcedar (*Juniperus virginianus*) glades in Tennessee.

Wet longleaf pine savanna and eastern upland longleaf pine forest in Louisiana.

Calcareous prairie, Fleming glade, shortleaf pine/oak-hickory forest, mixed hardwood-loblolly pine forest, eastern xeric sandhill woodland, and stream terrace sandy woodland/savanna in Louisiana.

Slash pine (*Pinus elliottii*) forests in southwestern Florida.

Red pine and white pine forests in Minnesota.

Coastal redwood (*Sequoia sempervirens*) forests in California.

Old-growth ponderosa pine (*Pinus ponderosa*) and eastside Cascades Mountains.

Riparian forests in California, Arizona, and New Mexico.

Coastal sage scrub (especially maritime) and coastal mixed chaparral in southern California.

Dry forest on main islands of Hawaii.

All types of native habitats in the lower delta of the Rio Grande River, Texas.

Tallgrass prairie (all types combined).

Native shrub and grassland steppe in Oregon and in Washington.

Low elevation grasslands in Montana.

Gulf Coast pitcher plant (*Sarracenia* spp.) bogs.

Pocosins (evergreen shrub bogs) and ultramafic soligenous wetlands in Virginia.

Mountain bogs (southern Appalachian bogs and swamp forest-bog complex) in Tennessee and in North Carolina.

Upland wetlands on the Highland Rim of Tennessee.

Saline wetlands in eastern Nebraska.

Wetlands (all types combined) in south-central California, Illinois, Indiana, Iowa, Missouri, Nebraska, and Ohio.

Marshes in the Carson-Truckee area of western Nevada.

Low-elevation wetlands in Idaho.

Woody hardwood draws, glacial pothole ponds, and peatlands in Montana.

Vernal pools in the Central Valley and in southern California.

Marshes in the Coos Bay area of Oregon.

Freshwater marsh and coastal salt marsh in Southern California.

Seasonal wetlands of the San Francisco Bay, California.

Large streams and rivers in all major regions.

Aquatic mussel (Unionidae) beds in Tennessee.

Submersed aquatic vegetation in the Chesapeake Bay, in Maryland, and in Virginia.

Mangrove swamps and salt marsh along the Indian River lagoon, Florida.

Seagrass meadows in Galveston Bay, Texas.

Threatened (70-84% decline)

Nationwide riparian forests (other than in already listed regions), including southern bottomland hardwood forests.

Xeric habitats (scrub, scrubby flatwoods, sandhills) on the Lake Wales Ridge, Florida.

Tropical hardwood hammocks on the central Florida keys.

Northern hardwood forest, aspen (*Populus* spp.) parkland, and jack pine (*Pinus banksiana*) forests in Minnesota.

Saline prairie, western upland longleaf pine forest, live oak-pine-magnolia (*Quercus virginiana*-*Pinus* spp.-*Magnolia* spp.) forest, western xeric sandhill woodland, slash pine-pond baldcypress-hardwood (*Pinus elliottii*-*Taxodium ascendens*) forest, wet and mesic spruce-pine (*P. glabra*)-hardwood flatwoods, wet mixed hardwood-loblolly pine (*Pinus taeda*) flatwoods, and flatwoods ponds in Louisiana.

Alvar grassland, calcareous pavement barrens, dwarf pine ridges, mountain spruce-fir forest, inland Atlantic whitecedar swamp, freshwater tidal swamp, inland salt marsh, patterned peatland, perched bog, pitch pine-blueberry (*Pinus rigida*-*Vaccinium* spp.) peat swamp, coastal plain poor fens, rich graminoid fen, rich sloping fen, and riverside ice meadow in New York.

Maritime-like forests in the Clearwater Basin of Idaho.

Woodland and chaparral on Santa Catalina Island.

Southern tamarack (*Larix laricina*) swamp in Michigan.

Wetlands (all kinds) in Arkansas, Connecticut, Kentucky, and Maryland.

Marshes in the Puget Sound region, Washington.

Cienegas (marshes) in Arizona.

Coastal wetlands in California.

Appendix C. Federally listed, proposed to be listed, and candidate animal and plant species associated with late-successional forests in western Oregon, Washington, and northwestern California. This list omits species not restricted to late-successional forests but associated with other habitats in the forest landscape that may be affected by forest management. From unpublished data, U.S. Fish and Wildlife Service, Portland, Oregon (Gary Miller, U.S. Fish and Wildlife Service, personal communication).

Listed Species

Resident Fishes

Oregon chub (*Oregonichthys crameri*)E.

Birds

Marbled murrelet (*Brachyramphus marmoratus*)T.

Bald eagle (*Haliaeetus leucocephalus*)E.

Northern spotted owl (*Strix occidentalis caurina*)T.

Candidate and Proposed Species

Plants

Wayside aster (*Aster vialis*)2.

Bensonia (*Bensoniella oregana*)2.

Mt. Mazama collomia (*Collomia mazama*)2.

Cold-water corydalis (*Corydalis aquae-gelidae*)2.

Mollusks

California floater mussel (*Anodonta californiensis*).

Columbia pebblesnail or great Columbia river spire snail (*Fluminicola* (= *Lithoglyphus*) *columbiana*) 2.

Snail (*Monadenia fidelis minor*)2.

Trinity bristlesnail or California northern river snail (*Monadenia setosa*) 2.

Columbia pebblesnail or spire snail (*Monadenia troglodytes troglodytes*) 2.

Resident Fishes

Olympic mudminnow (*Novumbra hubbsi*)2.

McCloud redband trout (*Oncorhynchus mykiss* ssp.)2.

Bull trout (*Salvelinus confluentus*)2.

Amphibians

Shasta salamander (*Hydromantes shastae*)2.

Del Norte salamander (*Plethodon elongatus*)2.

Larch mountain salamander (*Plethodon larselli*)2.

Siskiyou mountain salamander (*Plethodon stormi*)2.

Birds

Harlequin duck (*Histrionicus histrionicus*)2.

Northern goshawk (*Accipiter gentilis*)2.

Mammals

White-footed vole (*Arborimus albipes*)2.

Lynx (*Felis lynx canadensis*)2.

Pacific fisher (*Martes pennanti pacifica*)2.

Pacific western big-eared bat (*Plecotus townsendii townsendii*)2.

[E = Listed Endangered, T = Listed Threatened, PE = Proposed Endangered, 2 = Candidate Category 2 (taxa that existing information indicates may warrant listing but for which substantial biological data in support of a proposed rule are lacking).]

Appendix D. Federally listed, proposed to be listed, and candidate animal and plant species associated with coastal sage scrub in southern California. This list omits species restricted to unique patch habitats (e.g., vernal pools) in the coastal sage scrub landscape mosaic. From Scientific Review Panel (1992) and unpublished data, California Department of Fish and Game, Natural Diversity Data Base, Sacramento, California.

Listed Species

Birds

California gnatcatcher (*Polioptila californica californica*)T.

Mammals

Stephens' kangaroo rat (*Dipodomys stephensi*)E.

Candidate Species

Plants

San Diego thorn mint (*Acanthomintha ilicifolia*)1.

Munz's onion (*Allium fimbriatum* var. *munzii*)1.

Aphanisma (*Aphanisma blitoides*)2.

San Diego ambrosia (*Ambrosia pumila*)2.

Braunton's milk vetch (*Astragalus brauntonii*)2.

- Dean's milk vetch (*Astragalus deani*)2.
- Payson's jewelflower (*Caulanthus simulans*)2.
- Orcutt's spineflower (*Chorizanthe orcuttiana*)1.
- San Fernando Valley spineflower (*Chorizanthe parryi* var. *fernandina*)1.
- Parry's spineflower (*Chorizanthe parryi* var. *parryi*)2.
- Orcutt's bird's-beak (*Cordylanthus orcuttianus*)2.
- Del Mar Mesa sand aster (*Corethrogyne filaginifolia* var. *linifolia*)2.
- Western dichondra (*Dichondra occidentalis*)2.
- Orcutt's dudleya (*Dudleya attenuata* ssp. *orcuttii*)2.
- Short-leaved dudleya (*Dudleya brevifolia*)1.
- Many-stemmed dudleya (*Dudleya multicaulis*)2.
- Conejo dudleya (*Dudleya parva*)1.
- Laguna Beach dudleya (*Dudleya stolonifera*)1.
- Variegated dudleya (*Dudleya variegata*)2.
- Verity's dudleya (*Dudleya verityi*)2.
- Bright green dudleya (*Dudleya virens*)2.
- Sticky dudleya (*Dudleya viscida*)1.
- Conejo buckwheat (*Eriogonum crocatum*)2.
- San Diego barrel cactus (*Ferocactus viridescens*)2.
- Palmer's haplopappus (*Haplopappus palmeri* ssp. *palmeri*)2.
- Orcutt's hazardia (*Hazardia orcuttii*)2.
- Otay tarplant (*Hemizonia conjugens*)2.
- Santa Susana Mountains tarplant (*Hemizonia minthornii*)2.
- Nevin's barberry (*Mahonia nevinii*)1.
- Davidson's bush-mallow (*Malacothamnus davidsonii*)2.
- San Diego goldenstar (*Muilla clevelandii*)2.
- Willowy monardella (*Monardella linoides* ssp. *viminea*)2.

Pringle's monardella (*Monardella pringlei*)1.

Short-lobed broomrape (*Orobanche parishii* ssp. *brachyloba*)2.

Pringle's yampah (*Perideridia pringlei*)3.

Insects

Quino checkerspot butterfly (*Euphydryas editha quino*)1.

Hermes copper butterfly (*Lycaena hermes*)2.

Reptiles

Orange-throated whiptail (*Cnemidophorus hyperythrus*)2.

Coastal western whiptail (*Cnemidophorus tigris multiscutatus*)2.

San Diego banded gecko (*Coleonyx variegatus abbotti*)2.

Red diamond rattlesnake (*Crotalus ruber*)2.

Coastal rosy boa (*Lichanura trivirgata rosafusca*)2.

San Diego horned lizard (*Phrynosoma coronatum blainvillei*)2.

Coast patch-nosed snake (*Salvadora hexalepis virgultea*)2.

Birds

Southern California rufous-crowned sparrow (*Aimophila ruficeps canescens*)2.

Bell's sage sparrow (*Amphispiza belli belli*)2.

San Diego cactus wren (*Campylorhynchus brunneicapillus sandiegoensis*)2.

Mammals

Dulzura California pocket mouse (*Chaetodipus californicus femoralis*)2.

San Bernardino kangaroo rat (*Dipodomys merriami parvus*)2.

San Diego black-tailed jack rabbit (*Lepus californicus bennettii*)2.

Southern grasshopper mouse (*Onychomys torridus ramona*)2.

Los Angeles pocket mouse (*Perognathus longimembris brevinasus*)2.

Pacific pocket mouse (*Perognathus longimembris pacificus*)2.

[E = Listed Endangered, T = Listed Threatened, 1 = Candidate Category 1 (taxa for which the U.S. Fish and Wildlife Service has sufficient biological information in support of a listing proposal, 2 = Candidate category 2 (taxa for which existing information

indicates listing but for which substantial biological data in support of a proposed rule are lacking).]

Appendix E. Federally listed, proposed to be listed, and candidate animal and plant species associated with longleaf pine (*Pinus palustris*) or wiregrass (*Aristida stricta*) from Noss (1988), Hardin and White (1989), and unpublished data from state natural-heritage programs (N.C., S.C., Ga., Fla., Ala., Miss., La.) with updated status information from Federal Register 50 FR Part 17 (September 1993), natural-heritage programs, and from issues of the *Endangered Species Technical Bulletin* (1989-1994).

Listed Species

Plants

Apalachicola rosemary (*Conradina glabra*) E.

Pigeon-wing (*Clitoria fragrans*) T.

Beautiful pawpaw (*Deeringothamnus pulchellus*) E.

Rugel's pawpaw (*Deeringothamnus rugellii*) E.

Scrub mint (*Dicerandra frutescens*) E.

Scrub buckwheat (*Eriogonum longifolium* var. *gnaphalifolium*) T.

Harper's beauty (*Harperocallis flava*) E.

Rough-leaf loosestrife (*Lysimachia asperulifolia*) E.

Britton's bear-grass (*Nolina brittonia*) E.

Godfrey's butterwort (*Pinguicula ionantha*) T.

Chapman's rhododendron (*Rhododendron chapmanii*) E.

Michaux's sumac (*Rhus michauxii*) E.

Green pitcherplant (*Sarracenia oreophila*) E.

Chaffseed (*Schwalbea americana*) E.

Gentian pinkroot (*Spigelia gentianoides*) E.

Cooley's meadowrue (*Thalictrum cooleyi*) E.

Clasping warea (*Warea amplexifolia*) E.

Carter's warea (*Warea carteri*) E.

Reptiles

Gopher tortoise (*Gopherus polyphemus*)T³.

Sand skink (*Neoeceps reynoldsi*)T.

Indigo snake (*Drymarchon corais couperi*)T.

Blue-tailed mole skink (*Eumeces egregius lividus*)T.

Birds

Mississippi sandhill crane (*Grus canadensis pulla*)E.

Bald eagle (*Haliaeetus leucocephalus*)E.

Florida scrub jay (*Aphelocoma coerulescens coerulescens*)T.

Red-cockaded woodpecker (*Picoides borealis*)E.

Mammals

Florida panther (*Felis concolor coryi*)E.

Candidate and Proposed Species

Plants

Incised groovebur (*Agrimonia incisa*)2.

Carolina lead-plant (*Amorpha georgiana* var. *confusa*)2.

Georgia lead-plant (*Amorpha georgiana* var. *georgiana*)2.

Southern three-awned grass (*Aristida simpliciflora*)2.

Southern milkweed (*Asclepias viridula*)2.

Chapman's aster (*Aster chapmani*)2.

Coyote-thistle aster (*Aster eryngiifolius*)2.

Pine-woods aster (*Aster spinulosus*)2.

Sandhills milk-vetch (*Astragalus michauxii*)2.

Purple balduina (*Balduina atropurpurea*)2.

Hairy wild-indigo (*Baptisia calycosa* var. *villosa*)2.

Scare-weed (*Baptisia simplicifolia*)2.

Ashe's savory (*Calamintha ashei*)2.
Sand grass (*Calamovilfa curtissii*)2.
Piedmont jointgrass (*Coelorachis tuberculosa*)2.
Large-flowered rosemary (*Conradina grandiflora*)2.
Tropical waxweed (*Cuphia aspera*)2.
Umbrella sedge (*Cyperus grayoides*)2.
Dwarf burhead (*Echinodorus parvulus*)2.
Telephus spurge (*Euphorbia telephioides*)PT.
Wiregrass gentian (*Gentiana pennelliana*)2.
Florida beardgrass (*Gymnopogon floridanus*)2.
Hartwrightia (*Hartwrightia floridana*)2.
Mock pennyroyal (*Hedeoma graveolens*)2.
Spider-lily (*Hymenocallis henryae*)2.
Thick-leaved water-willow (*Justicia crassifolia*)2.
White-wicky (*Kalmia cuneata*)2.
Tiny bog buttons (*Lachnocaulon digynum*)2.
Pine pinweed (*Lechea divaricata*)2.
Godfrey's blazing star (*Liatris provincialis*)2.
Slender gay-feather (*Liatris tenuis*)2.
Panhandle lily (*Lilium iridollae*)2.
Bog spicebush (*Lindera subcoriacea*)2.
Large-fruited flax (*Linum macrocarpum*)2.
Harper's grooved-yellow flax (*Linum sulcatum* var. *harperi*)2.
West's flax (*Linum westii*)2.
Boykin's lobelia (*Lobelia boykinii*)2.
White birds-in-a-nest (*Macbridea alba*)PT.
Carolina bogmint (*Macbridea caroliniana*)2.

- Southern marshallia (*Marshallia ramosa*)2.
- Bog asphodel (*Narthecium americanum*)1.
- Fall-flowering ixia (*Nemastylis floridana*)2.
- Florida bear-grass (*Nolina atopocarpa*)2.
- Savanna cowbane (*Oxypolis ternata*)2.
- Naked-stemmed panic grass (*Panicum nudicaule*)2.
- Carolina grass-of-parnassus (*Parnassia caroliniana*)2.
- Wavyleaf wild quinine (*Parthenium radfordii*)2.
- Chapman's butterwort (*Pinguicula planifolia*)2.
- Bent golden-aster (*Pityopsis flexuosa*)2.
- Pineland plantain (*Plantago sparsiflora*)2.
- Wild coco, eulophia (*Pteroglossaspis ecristata*)2.
- Sandhills pixie-moss (*Pyxidantha barbulata* var. *brevifolia*)2.
- St. John's Susan, yellow coneflower (*Rudbeckia nitida* var. *nitida*)2.
- Bog coneflower (*Rudbeckia scabrifolia*)2.
- White-top pitcherplant (*Sarracenia leucophylla*)2.
- Wherry's pitcherplant (*Sarracenia rubra* ssp. *wherryi*)2.
- Florida skullcap (*Scutellaria floridana*)PT.
- Scarlet catchfly (*Silene subciliata*)2.
- Carolina goldenrod (*Solidago pulchra*)2.
- Spring-flowering goldenrod (*Solidago verna*)2.
- Wireleaf dropseed (*Sporobolus teretifolius*)2.
- Pickering's morning-glory (*Stylisma pickeringii*)2.
- Pineland hoary-pea (*Tephrosia mohrii*)2.
- Smooth bog-asphodel (*Tofieldia glabra*)2.
- Shinner's false-foxglove (*Tomanthera (Agalinis) pseudaphylla*)2.

Least trillium (*Trillium pusillum* (5 varieties)2).

Chapman's crownbeard (*Verbesina chapmanii*)2.

Variable-leaf crownbeard (*Verbesina heterophylla*)2.

Drummond's yellow-eyed grass (*Xyris drummondii*)2.

Harper's yellow-eyed grass (*Xyris scabrifolia*)2.

Insects

Buchholz's dart moth (*Agrotis buchholzi*)2.

Aphodius tortoise commensal scarab beetle (*Aphodius troglodytes*)2.

Arogos skipper (*Atrytone arogos arogos*)2.

Copris tortoise commensal scarab beetle (*Copris gopheri*)2.

Sandhills clubtail dragonfly (*Gomphus parvidens carolinus*)2.

Spiny Florida sandhill scarab beetle (*Gronocarus multispinosus*)2.

Prairie mole cricket (*Gryllotalpa major*)2.

Mitchell's satyr (*Neonympha mitchellii francisci*)2.

Onthophagus tortoise commensal scarab beetle (*Onthophagus polyphemi*)2.

Carter's noctuid moth (*Spartiniphaga carterae*)2.

Amphibians

Flatwoods salamander (*Ambystoma cingulatum*)2.

Gopher frog (*Rana areolata*)2.

Carolina gopher frog (*Rana capito capito*)2.

Dusky gopher frog (*Rana capito sevosa*)1.

Reptiles

Gopher tortoise (*Gopherus polyphemus*)2.

Florida scrub lizard (*Sceloporus woodi*)2.

Southern hognose snake (*Heterodon simus*)2.

Black pine snake (*Pituophis melanoleucus lodingi*)2.

Northern pine snake (*Pituophis melanoleucus melanoleucus*)2.

Florida pine snake (*Pituophis melanoleucus mugitus*)2.

Short-tailed snake (*Stilosoma extenuatum*)2.

Birds

Southeastern American kestrel (*Falco sparverius paulus*)2.

Loggerhead shrike (*Lanius ludovicianus*)2.

Bachman's sparrow (*Aimophila aestivalis*)2.

Henslow's sparrow (*Ammodramus henslowii*)2.

Mammals

Florida weasel (*Mustela frenata peninsulae*)2.

Florida black bear (*Ursus americanus floridanus*)2.

Florida mouse (*Peromyscus floridanus*)2.

Sherman's fox squirrel (*Sciurus niger shermani*)2.