Quantifying Threats to Imperiled Species in the United States

Assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease

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Biologists are nearly unanimous in their belief that humanity is in the process of extirpating a significant portion of the earth's species. The ways in which we are doing so reflect the magnitude and scale of human enterprise. Everything from highway construction to cattle ranching to leaky bait buckets has been implicated in the demise or endangerment of particular species. According to Wilson (1992), most of these activities fall into four major categories, which he terms "the mindless horsemen of the environmental apocalypse": overexploitation, habitat destruction, the introduction of non-native (alien) species, and the spread of diseases carried by alien species. To these categories may be added a fifth, pollution, although it can also be considered a form of habitat destruction.

Surprisingly, there have been relatively few analyses of the extent to which each of these factors—much less the more specific deeds encompassed by them—is responsible for endangering species. In general, scientists agree that habitat destruction is currently the primary lethal agent (Ehrlich 1988, Wilson 1992), followed by the spread of alien species (Wilson 1992). However, apart from several notable exceptions—including studies of North American fishes by Williams et al. (1989), endangered plants and animals in the United States by Flather et al. (1994, 1998), aquatic organisms by Richter et al. (1997), and imperiled birds by Collar et al. (1994)—few quantitative studies of threats to species have been conducted. More such studies are needed to provide conservationists, land stewards, and decision makers with a better understanding of the relationships between specific human activities and the loss of biodiversity.

Habitat loss is the single greatest threat to biodiversity, followed by the spread of alien species

In this article, we quantify the extent to which various human activities are imperiling plant and animal species in the United States. Our analysis has two parts: a coarse-scale examination of the numbers and types of US species imperiled by the major categories of threats, and a fine-scale analysis of the types of habitat destruction affecting US plants and animals protected under the federal Endangered Species Act (ESA). We also speculate on how these threats have changed over time and are likely to change in the future. We conclude with a brief discussion of the implications of our findings for the long-term protection of imperiled species in the United States.

An overview of the threats

To obtain an overview of the threats to biodiversity in the United States, we tabulated the number of species threatened by five categories of threats: habitat destruction, the spread of alien species, overharvest, pollution (including siltation), and disease (caused by either alien or native pathogens). We restricted this coarse-scale analysis to imperiled plants and animals occurring within the 50 states and falling into any of four categories: all full species of mammals, birds, reptiles, amphibians, and fish with status ranks of "possibly extinct," "critically imperiled," or "imperiled," as determined by The Nature Conservancy (TNC) in association with the Network of Natural Heritage Programs and Conservation Data Centers (Master 1991); all full species of freshwater mussels, butterflies and skippers, tiger beetles, and dragonflies and damselflies with status ranks of possibly extinct, critically imperiled, or imperiled, as determined by TNC; all full species of vascular plants with status ranks of possibly extinct or

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Table 1. Taxonomic breakdown of species used in the coarse-scale analysis. Included are species classified as imperiled by The Nature Conservancy and all species, subspecies, and populations that, as of January 1996, are listed as endangered or threatened under the Endangered Species Act or have been formally proposed for listing.

	Number of imperiled species	Number of imperiled species with threats data	Percentage of imperiled species with threats data
Vertebrates	541	494	91
Mammals	88	85	97
Birds	101	98	97
Reptiles	40	38	95
Amphibians	69	60	87
Fishes	243	213	88
Invertebrates	471	331	70
Dragonflies and damselflies	33	18	54
Freshwater mussels	150	102	68
Crayfish	110	67	61
Tiger beetles	8	6	75
Butterflies and skippers	46	33	72
Other invertebrates	124	104	84
Plants	1478	1055	71
Total	2490	1880	75

critically imperiled, as determined by TNC; and all species, subspecies, or vertebrate populations listed by the US Fish and Wildlife Service (USFWS) or the National Marine Fisheries Service as threatened or endangered or officially proposed for listing under the ESA as of 1 January 1996. (The ESA permits the listing of species and subspecies of plants and animals as well as "distinct population segments" of vertebrates.) A total of 2490 imperiled species, subspecies, and populations fit these criteria.

Information on the threats to each of these species, subspecies, and populations was obtained from a number of sources, including the *Federal Register* (i.e., the listing notices published for all species designated as threatened or endangered under the ESA), a survey of biologists conducted by Richter et al. (1997) for aquatic species, the Natural Heritage Central Databases managed by TNC, and interviews with specialists in particular species groups and geographical regions. We included only known threats and excluded potential or hypothetical ones. We did not attempt to distinguish between ongoing and historical threats, partly because such information is usually lacking and partly because the distinction itself is problematic in the case of habitat destruction. Nor did we try to distinguish between major and minor threats to each species because such information was not consistently available. In a few cases, it was impossible to assign a particular human activity to one of the major threat categories; we excluded these activities from our coarse-scale analysis.

We were able to obtain information on threats for 1880 (75%) of the 2490 imperiled species, subspecies, and populations that met our criteria for inclusion in this study (Table 1). (For 52 of the species, we could not identify any anthropogenic threats.) We used the resulting database to determine the relative significance of the major threats categories and to investigate differences between species groups in their vulnerability to particular threats. We compared the distribution of threats among plants and animals, among vertebrate and invertebrate animals, and within vertebrate classes. We also compared the distribution of threats among terrestrial and aquatic species, Hawaiian and mainland vascular plants, and Hawaiian and mainland birds. For all comparisons, statistical significance was assessed using the chi-squared contingency test (two-tailed).

We emphasize at the outset that there are some important limitations to the data we used. The attribution of a specific threat to a species is usually based on the judgment of an expert source, such as a USFWS employee who prepares a listing notice or a state Fish and Game employee who monitors endangered species in a given region. Their evaluation of the threats facing that species may not be based on experimental evidence or even on quantitative data. Indeed, such data often do not exist. With respect to species listed under the ESA, Easter-Pilcher (1996) has shown that many listing notices lack important biological information,

Table 2. Percentages of species in different groups that are imperiled by habitat degradation and loss, alien species, pollution, overexploitation, and disease. Categories are nonexclusive and therefore do not sum to 100.

Cause	All species (n = 1880)	Vertebrates (n = 494)	Invertebrates (n = 331)	Plants (n = 1055)	Mammals (n = 85)	Birds (n = 98)	Reptiles (n = 38)	Amphibians (n = 60)	Fishes (n = 213)	Freshwater mussels (n = 102)	Crayfish (n = 67)	Tiger beetles (n = 6)	Butterflies and skippers (n = 33)	Other invertebrates (n = 104)
Habitat degradation/loss	85	92	87	81	89	90	97	87	94	97	52	100	97	94
Alien species	49	47	27	57	27	69	37	27	53	17	4	0	36	52
Pollution	24	46	45	7	19	22	53	45	66	90	28	0	24	19
Overexploitation	17	27	23	10	45	33	66	17	13	15	0	33	30	46
Disease	3	11	0	1	8	37	8	5	1	0	0	0	0	0

including data on past and possible future impacts of habitat destruction, pesticides, and alien species. Depending on the species in question, the absence of information may reflect a lack of data, an oversight, or a determination by USFWS that a particular threat is not harming the species. The extent to which such limitations on the data influence our results is unknown.

Ranking the threats

Table 2 presents a summary of the percentages of species that are imperiled by habitat loss, alien species, pollution, overexploitation, and disease. Not surprisingly, habitat destruction and degradation emerged as the most pervasive threat to biodiversity, contributing to the endangerment of 85% of the species we analyzed (Figure 1). Indeed, habitat loss is the top-ranked threat (in terms of the number of species it affects) for all species groups. Competition with or predation by alien species is the second-ranked threat in the overall analysis, affecting 49% of imperiled species.

Alien species affect a higher proportion of imperiled plants (57%) than animals (39%); this difference is statistically significant (chi square = 60.23, d.f. = 1, $P<<0.001$). However, certain groups of animals (most notably birds and fish) appear to be as broadly affected as plants by alien species. There is also an unsurprising biogeographic component to the alien species problem: Higher proportions of Hawaiian birds and plants than continental birds and plants are threatened by alien species (Table 3, Figure 2). Similarly, a much higher proportion of Hawaiian birds is threatened by disease than is the case for continental birds. By contrast, nearly the same proportion of Hawaiian plants and continental plants are affected by disease (Table 3, Figure 3).

For all aquatic animal groups (amphibians, fish, dragonflies and damselflies, freshwater mussels, and crayfish), pollution is second only to habitat loss as a cause of endangerment. Our finding that a large number of aquatic species are threatened by pollution may reflect the fact that our definition of pollution includes siltation, which is one of the leading threats to aquatic biodiversity in North America (Richter et al. 1997).

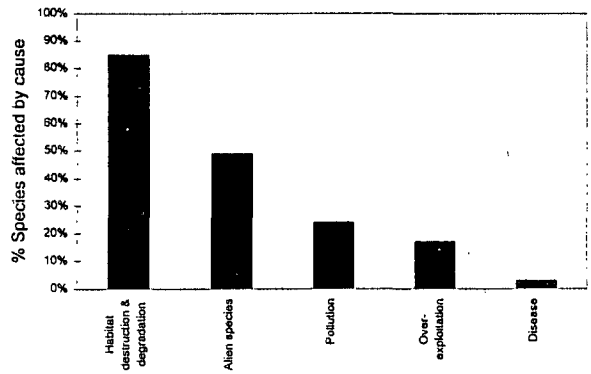

Figure 1. The major threats to biodiversity. Data refer to species classified as imperiled by The Nature Conservancy and to all endangered, threatened, and proposed species, subspecies, and populations protected under the Endangered Species Act. See also Table 2.

A closer look at habitat destruction

Given the primacy of habitat destruction as a threat to biodiversity, we examined its causes in greater detail. For this fine-scale analysis, we focused exclusively on US species, subspecies, and populations that have been added to the federal endangered species list or have been formally proposed for such listing by USFWS as of 1 January 1996. We focused on listed species because more information is usually available for them than for imperiled but unlisted species. We also included species that are federally listed or proposed for listing from Puerto Rico, the US Virgin Islands, and the Pacific Trust Territories. A total of 1207 species, subspecies, and populations was included in this phase of the analysis (Figure 4). (USFWS has listed as endangered all Hawaiian snails of the genus *Achatinella*. Approximately 41 species in that genus have been described to date, of which at least 18 are thought still to survive. However, USFWS did not treat these species individually in its formal listing notice in the *Federal Register*. For the purposes of this part of our analysis, we have therefore counted the entire genus as one "species.")

Categorizing habitat destruction. For the fine-scale analysis, we divided habitat destruction and degradation into 11 major categories (see box page 611). As in the coarse-scale analysis, we did not distinguish between current and historical threats or between major and minor threats. In many instances, the apparent threat to a species was actually spawned by another threat. Wherever possible, we attributed threats to their ultimate cause, based on the information in the *Federal Register*. For example, logging operations near a stream can lead to siltation, which is harmful to certain rare fishes and mussels. Thus, logging rather than siltation would have been scored as the threat to those fishes and mussels. For all comparisons of the prevalence of specific threats in different species groups, statistical significance was assessed using the chi-squared contingency test (two-tailed).

Again, we note some caveats with

Table 3. Percentages of imperiled birds and plants in Hawaii and in the continental United States that are threatened by habitat degradation and loss, alien species, pollution, overexploitation, and disease. Categories are nonexclusive and therefore do not sum to 100.

Cause	Continental US birds (n = 56)	Hawaiian birds (n = 42)	Continental US plants (n = 641)	Hawaiian plants (n = 414)
Habitat degradation/loss	88	93	90	66
Alien species	48	98	30	99
Pollution	38	2	12	0
Overexploitation	39	24	13	6
Disease	4	81	1	0

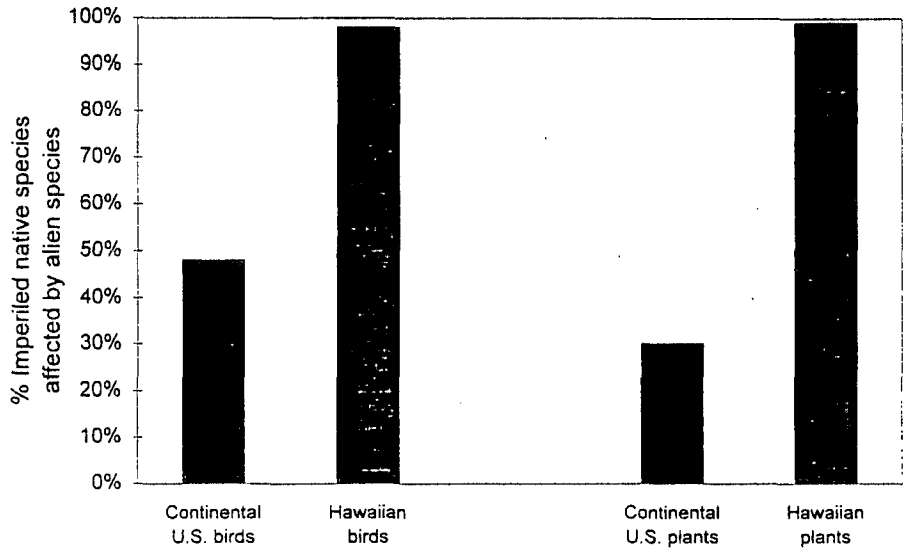

Figure 2. A comparison of the impacts of alien species on imperiled birds and plants in Hawaii and in the continental United States. A much higher proportion of Hawaiian birds and plants than continental birds and plants is threatened by alien species (chi-square = 27.60, d.f. = 1, P <<0.001 for birds; chi-square = 484.28, d.f. = 1, P<<0.001 for plants). Data are taken from Table 3.

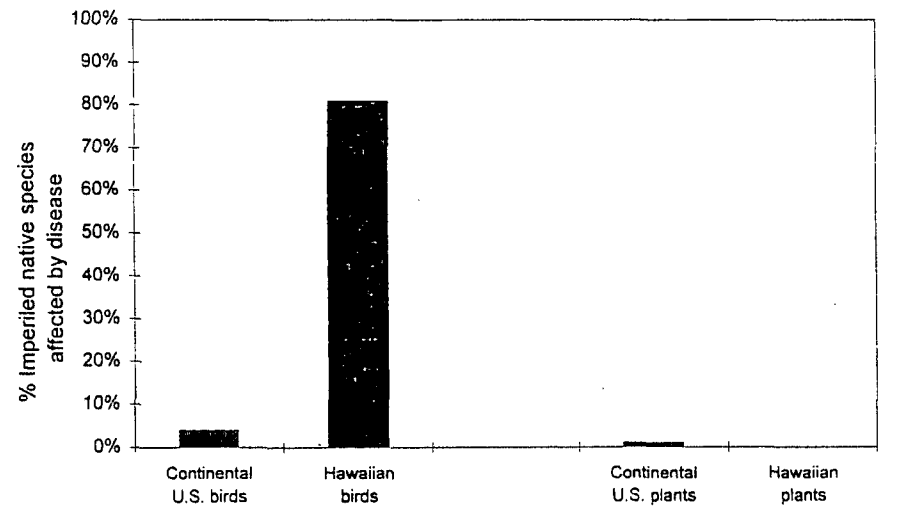

Figure 3. A comparison of the impacts of disease on imperiled birds and plants in Hawaii and in the continental United States. A much higher proportion of Hawaiian birds than continental birds is threatened by disease (chi-square = 62.03, d.f. = 1, P<<0.001). By contrast, similar proportions of Hawaiian and continental plants are affected by disease (although the difference is statistically significant: chi-square = 4.02, d.f. = 1, P = .045).

respect to the data in this phase of the analysis. Species added to the endangered list prior to 1980 (238 species) tended to have fewer threats delineated in the listing notices than species listed in later years. Although there may be a biological basis for this difference, we strongly suspect that it reflects the less controversial nature of endangered species protection at that time. Before 1980, USFWS probably was under less pressure to produce detailed justifications for its listing decisions. We do not know how this pattern may have influenced our results. Also, as noted in our coarse-scale analysis, assessments of the threats to individual species are often based on the subjective opinions of knowledgeable individuals, rather than experimental evidence or quantitative data.

Ranking the causes of habitat destruction. The most overt and widespread forms of habitat alteration were, as might be expected, the leading threats to species that are either listed or proposed for listing (hereafter referred to collectively as "endangered" species), as measured by the number of species they affect (Table 4). These forms include agriculture (affecting 38% of endangered species), commercial development (35%), water development (30% when agricultural diversion is included; 17% for just dams, impoundments, and other barriers), and infrastructure development (17%). Not surprisingly, the impacts of water development are felt most acutely by aquatic species. Ninety-one percent of endangered fish and 99% of endangered mussels are affected by water development, in contrast to 10% of mammals and 22% of birds. Within the category of infrastructure development, roads affect a wide array of species (15% of all endangered species), confirming their reputation as "a leading threat to biodiversity" (Noss and Cooperrider 1994).

Outdoor recreation also harms a large number of endangered species (27%). It affects a significantly higher proportion of plants than animals (33% vs. 17%; chi square = 39.03, d.f. = 1, P<<0.001). Within the category of outdoor recreation, the use of off-road vehicles is implicated in the demise of approximately 13% of endangered species.

Among extractive land uses, logging, mining, and grazing have contributed to the demise of 12%, 11%, and 22%, respectively, of the endangered species we analyzed. Both logging and mining are especially serious threats to freshwater mussels, probably because they result in increased amounts of silt, in the cases of both logging and mining, and of toxic pollutants, in the case of mining. Livestock grazing, on the other hand, is particularly harmful to plants, affecting 33% of endangered plant species compared to 14% of endangered animals; the difference is highly significant (chi square = 51.95, d.f. = 1, P<<0.001).

Finally, 168 species (14%) are threatened by disruption of fire regimes in the ecosystems in which they live. Of these, 85 (7%) are

threatened by fire suppression and 83 (7%) are threatened by controlled or uncontrolled fires.

Comparisons with other studies

Flather et al. (1994, 1998) catalogued the threats to US endangered species based on information from the *Federal Register*, the USFWS *Endangered Species Technical Bulletin*, recovery plans for individual species, federal agency reports, and consultations with USFWS biologists and state Natural Heritage Program scientists. Their analysis covered 667 species, subspecies, and populations protected by the ESA as of August 1992; it did not include species proposed for listing.

Although the way in which Flather et al. categorized threats was not identical to our approach, the major findings from the two studies can still be compared. These authors also identified habitat loss and alien species as the two most widespread threats to endangered species, affecting more than 95% and 35% of listed species, respectively. (Comparable figures from our study are 85% for habitat destruction and 49% for alien species.) The smaller percentage of species affected by exotics in Flather et al.'s study probably reflects the large number of Hawaiian species that were included in our study but were not on the endangered species list at the time Flather et al. conducted theirs. Flather et al. (1998) also point out that the relative frequency of particular threats to species varies geographically.

Two previous studies have focused on threats to aquatic species. Williams et al. (1989) catalogued threats to 364 species and subspecies of imperiled fish from Canada, the United States, and Mexico; Richter et al. (1997) surveyed aquatic biologists to identify the threats to 135 imperiled freshwater fishes, crayfishes, dragonflies and damselflies, mussels, and amphibians in the United States. Narrowing the scope of Williams et al. to imperiled US and Canadian fishes (254 species), we can compare their results with ours. The findings of the two studies are similar: Williams et al. identified habitat destruction and degradation as the most widespread threat to imperiled fishes, affecting 96% of the species (versus 94% in our study; Table 2). Next in significance was an amalgamated category of hybridization, alien species, predation, and competition, which affected 39% of the fish species (versus our tally of 53% for alien species, which probably covers most of the same threats). Finally, Williams et al. found that overharvest and disease affected 4% and 2%, respectively, of the fishes (versus 13% and 1% in our study).

Richter et al. (1997) concluded that the three leading threats to aquatic species nationwide were agricultural nonpoint pollution (e.g., siltation and nutrient inputs), alien species, and altered hydrologic regimes due to dams and impoundments. This conclusion is consistent with our findings from the fine-scale analysis, which identified pollution and impoundments (including dams) as significant threats to fish and mus-

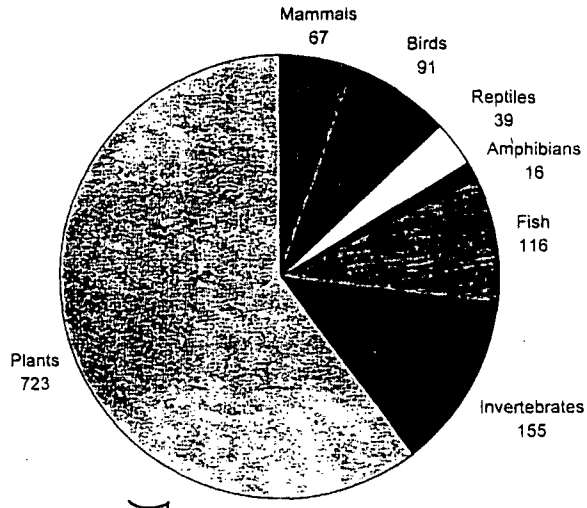

Figure 4. Taxonomic breakdown of the species, subspecies, and populations used in the fine-scale analysis. The 1207 species, subspecies, and populations include those that are listed as endangered or threatened under the Endangered Species Act or are proposed for listing.

The major categories of habitat destruction used in this analysis

- Agriculture (including agricultural practices, land conversion and water diversion for agriculture, pesticides and fertilizers; excluding livestock grazing)
- Livestock grazing (including range management activities)
- Mining, oil and gas, and geothermal exploration and development (including roads constructed for and pollutants generated by these activities)
- Logging (including impacts of logging roads and forest management practices)
- Infrastructure development (including bridges, dredging for navigation, and road construction and maintenance)
- Road construction and maintenance specifically (including logging and mining roads)
- Military activities
- Outdoor recreation (including swimming, hiking, skiing, camping, and off-road vehicles)
- Off-road vehicles specifically
- Water development (including diversion for agriculture, livestock, residential use, industry, and irrigation; dams, reservoirs, impoundments, and other barriers to water flow; flood control; drainage projects; aquaculture; navigational access and maintenance)
- Dams, impoundments, and other barriers to water flow specifically
- Pollutants (including siltation and mining pollutants)
- Land conversion for urban and commercial development
- Disruption of fire ecology (including fire suppression)

sels (Table 4). Our coarse-scale analysis, which included a larger pool of imperiled species than the fine-scale analysis, also highlighted the importance of alien species as a threat to US fish.

Richter et al. (1997) point out that there are important geographic differences in the nature of the threats facing aquatic species. Aquatic species in the eastern United States are experiencing particular harm from agricultural nonpoint pollution; in the West, the dominant threat is alien species, followed by habitat degradation and altered hydrologic regimes. Richter et al. attribute these differences to differences in both land use patterns in the East versus the West and in the ecological sensitivities of eastern versus western species.

Using information from USFWS recovery plans, Schemske et al. (1994) identified the primary cause of endangerment for each of 98 US plant species protected under the ESA. These authors did not distinguish between historical and contemporary threats, and they listed only one (i.e., the primary) threat per species, although they acknowledged that most species experience more than one threat. The top six threats in their study (in terms of frequency of appearance) were development (affecting 20.4% of the species); grazing (10.2%); collecting (10.2%); water control (8.2%); oil, gas, and mining (8.2%); and trampling (8.2%). By contrast, our coarse-scale analysis identified habitat destruction and alien species as the two most widespread threats to imperiled plants, affecting 81% and 57% of species, respectively. Moreover, in our fine-scale analysis of habitat destruction, the top five threats to imperiled plants protected under the ESA were land conversion (i.e., development; 36%), agriculture (33%), grazing (33%), outdoor recreation (33%), and disruption of fire ecology (20%).

The consistently higher percentages for all threats in our study compared to that of Schemske et al. (1994) undoubtedly stem from our practice of tallying multiple threats per species. Perhaps the most noticeable difference between the two studies lies in their assessments of the importance of alien species as a threat to rare plants. Schemske et al. (1994) considered alien species the primary threat to only 6.1% of the plants they studied, whereas we found that 57% of endangered plants were affected by alien species. Their lower percentage stems in part from the small number of Hawaiian plants that had been listed as endangered or threatened at the time of their study. Our results do indicate that alien species are a frequent threat to continental plants as well (Table 3), but they are not necessarily the primary threat, which may account for the remainder of the difference.

Collar et al. (1994) identified the primary threat to each of 1111 bird species they regarded as imperiled. Because they evaluated endangered birds worldwide, focused on primary threats only, and categorized the

Table 4. Percentages of federal endangered, threatened, or proposed species, subspecies, or populations that are harmed by various types of habitat destruction and degradation. Categories are nonexclusive and therefore do not sum to 100.

Cause	Overall (n = 1207)	Vertebrates (n = 329)	Invertebrates (n = 155)	Plants (n = 723)	Mammals (n = 67)	Birds (n = 91)	Reptiles (n = 39)	Amphibians (n = 16)	Fish (n = 116)	Insects (n = 39)	Arachnids (n = 4)	Crustaceans (n = 20)	Mollusks (n = 23)	Mussels (n = 69)
Agriculture	38	40	57	33	25	42	33	63	45	56	75	55	35	64
Livestock grazing	22	17	10	33	19	20	8	19	16	15	0	30	9	1
Mining, oil and gas, geothermal	11	12	31	11	2	3	13	13	23	10	0	0	17	58
Logging	12	16	25	7	12	18	13	19	19	5	25	5	13	46
Infrastructure development (including roads)	17	16	12	20	9	8	28	38	17	23	25	10	9	6
Road construction and maintenance	15	15	10	17	8	8	23	38	16	18	25	5	9	6
Military activities	4	2	1	5	2	3	5	0	0	0	0	5	4	0
Outdoor recreation (including ORVs)	27	16	19	33	18	15	31	25	9	41	0	30	26	4
Off-road vehicles	13	6	12	16	6	7	13	13	1	31	0	25	4	0
Water development (including dams, etc.)	30	47	66	15	10	22	28	63	91	21	0	70	48	99
Dams, impoundments, and other barriers	17	28	54	5	3	9	15	13	64	15	0	15	35	96
Pollutants	20	27	66	7	5	10	21	25	55	26	75	55	48	97
Land conversion for commercial development	35	30	42	36	31	33	56	44	16	67	75	65	13	29
Disruption of fire ecology	14	5	6	20	7	8	5	6	0	18	25	0	4	0

threats differently than we did, their results are not directly comparable to ours. Nonetheless, it is worth noting that both studies identified habitat loss as the most widespread threat. In Collar et al.'s study, the next most important threats, in order of decreasing frequency, were small range or population, overhunting, and alien species. In our study, the next most important threats, also in order of decreasing frequency, were alien species, disease, overhunting, and pollution. The higher rankings accorded alien species and diseases in our analysis are probably due to the Hawaiian avifauna, which constitutes a large fraction of endangered birds in the United States and is profoundly affected by these threats. In our study, we did not classify small range per se as a threat.

Changes in threats over time

As human activities and customs change over time, one would expect to see corresponding changes in the threats to biodiversity. Because our study does not distinguish between historical and contemporary threats, it is not well suited to test this hypothesis. For example, the relatively large percentage of species affected by overexploitation (17%) includes a variety of animals that were once hunted but are now reasonably well protected from this threat (e.g., the whooping crane [*Grus americana*] and the California condor [*Gymnogyps californianus*]). Similarly, pesticide pollution is listed as the primary threat to the bald eagle (*Haliaeetus leucocephalus*) and to North American populations of the peregrine falcon (*Falco peregrinus*), but the primary pollutant harming both species—DDT—has been banned in the United States since 1972 (although it continues to be used in other countries where peregrines spend the winter). Thus, our study may overestimate the number of animals that are currently harmed by overexploitation and pollutants.

There are no accurate figures on the total number of alien species now established in the United States, although the Office of Technology Assessment [OTA] (1993) has estimated that there are at least 4500 (a number that OTA acknowledges is probably an underestimate). What is indisputably clear, however, is that the cumulative number of alien species in the United States has skyrocketed since the late 18th century (Sailer 1978, OTA 1993); this pattern holds for all types of species, from plants, to insects, to vertebrates. Given that the cumulative number of alien species is increasing over time, one may confidently predict that alien species will pose an ever-increasing threat to native flora and fauna.

A somewhat more complicated question is whether the *rate* of alien introductions has increased over time, which would indicate a rapidly worsening situation for imperiled species. The data from published studies are ambiguous on this point. Reviewing the numbers of alien terrestrial vertebrates, fishes, mollusks, and plant pathogens added to the United States per decade over the past 50 years, OTA (1993) found no consistent increase for any of the groups. The greatest numbers of terrestrial vertebrates and fishes were added during the 1950s and 1960s, whereas the 1970s saw the greatest increase in the numbers of mollusks and plant pathogens. On the other hand, a detailed study of alien species in the San Francisco Estuary shows that there have been more introductions in recent years than in earlier years (Cohen and Carlton 1995).

Many factors influence the rate at which alien species are introduced into the United States, so the lack of a consistent increase in that rate over time should not be surprising. Species can be brought into the country and released intentionally, or their release can occur as an unintentional byproduct of cultivation, commerce, tourism, or travel. Each new development in the field of transportation creates new opportunities for the transport of alien species, from the first sailing ships to reach US shores, to the building of the nation's road and highway system, to the advent of jet airplanes. As transporation technology changes, so do the opportunities for alien stowaways. Empty cargo ships arriving in the United States, for example, used to carry dry ballast in the form of rocks and soil, which was then off-loaded around wharves to provide cargo space. Numerous insects and plants were accidentally introduced into the United States in this dry ballast, including fire ants (*Solenopsis invicta* and *Solenopsis richteri*) and purple loosestrife (*Lythrum salicaria*). Today, ships use water for ballast instead of dry material, thus ending the spread of alien species via dry ballast. However, the release of ballast water into US waterways has been implicated in the introduction of at least eight alien species since 1980, including the zebra mussel, *Dreissena polymorpha* (OTA 1993). Finally, the public's growing infatuation with ornamental plants, tropical fish, and tropical birds has led to numerous unintentional releases of alien species, including over 300 plants in California alone (McClintock 1985).

Looking ahead, as the human population of the United States continues to grow, one might predict an increase in the frequency of biodiversity threats associated with urbanization, such as infrastructure development, water development, and land conversion. Comparable increases in the proportion of species affected by agriculture are also a possibility. There is, in fact, good reason to suspect that a growing human population in the United States will disproportionately affect this nation's imperiled species. Dobson et al. (1997) have shown that most endangered species in the United States are clustered in a relatively small number of areas, particularly in Hawaii, Southern California, and Florida. The human populations in all three states are projected to increase at rates well beyond the national average. Thus, whereas the population of the United States as a whole is expected to grow by 14% between 1995 and 2010, the populations of Hawaii, California, and Florida are projected to increase by 27%, 27%, and 22%, respectively (US Bureau of the Census 1995).

Although climate change was not listed as a current threat to any species in our databases, it is almost certain to become one in the foreseeable future due to increasing concentrations of greenhouse gases from fossil-fuel use, land-use changes, and agriculture. Climate models developed by the Intergovernmental Panel on Climate Change predict a 0.9–

3.5 °C increase in global mean temperature over the course of the next century (Houghton et al. 1995). That increase will cause a rise in sea levels of 15–95 cm and significant changes in the frequencies of severe floods and droughts.

These changes are likely to affect a broad array of imperiled species. For example, Morse et al. (1993) estimate that 7–11% of North America's vascular plant species would no longer encounter a suitable climatic regime ("climate envelope") within their present ranges in the event of a 3 °C increase in temperature. Due to their small ranges and weak dispersal abilities, imperiled plants would be disproportionately affected. Morse et al. (1993) also estimate that 10–18% of North America's rare plants could be excluded from their climate envelope due to climate change.

In another well-publicized study, Britten et al. (1994) noted that relictual populations of the critically endangered Uncompahgre fritillary butterfly (*Boloria acrocnema*) living atop a few peaks in the San Juan Mountains of southwestern Colorado were extremely vulnerable to unusual weather events. They further hypothesized that a regional warming trend (as might occur due to global climate change) could eliminate all of the butterfly's habitat, essentially pushing it off of the mountains and into extinction. Indirect support for this hypothesis comes from a recent study of another butterfly. Parmesan (1996) censused populations of the Edith's checkerspot (*Euphydryas editha*) throughout its known range (Baja California, the western United States, and western Canada) and found significant latitudinal and altitudinal differences in the proportion of populations (in suitable habitat) that had become extinct. Populations in Mexico were four times more likely to have vanished than those in Canada, a North–South gradient in survival that is consistent with the predicted impacts of global warming on species' ranges.

Conservation implications

The major findings of this study confirm what most conservation biologists have long suspected: Habitat loss is the single greatest threat to biodiversity, followed by the spread of alien species. However, the discovery that nearly half of the imperiled species in the United States are threatened by alien species—combined with the growing numbers of alien species—suggests that this particular threat may be far more serious than many people have heretofore believed. The impact of alien species is most acute in the Hawaiian Islands, as demonstrated by the fact that nearly 100% of the archipelago's imperiled plants and birds are threatened by alien species, compared with 30% and 48%, respectively, for mainland plants and birds (Table 3). This finding is also consistent with numerous other studies that have highlighted the unique vulnerability of island communities to alien species (Culliney 1988, Simberloff 1995).

Pollution (including siltation) ranks well below alien species as a threat to imperiled species in general, but it exceeds alien species as a threat to aquatic taxa. As Richter et al. (1997) point out, the pollutants affecting the largest number of aquatic species are agricultural pollutants, such as silt and nutrients, that enter lakes and rivers as runoff from farming operations. These nonpoint source pollutants have proved to be exceedingly difficult to regulate and control (Young and Congdon 1994).

Finally, this study and one by Wilcove and Chen (in press) raise troubling questions about the future of imperiled species in the United States. Both studies found that a high proportion of imperiled species is threatened by either fire suppression within their fire-maintained habitats or alien species. Both types of threats must be addressed through active, "hands-on" management of the habitat, such as pulling up alien plants and trapping alien animals or using prescribed fire to regenerate early successional habitats. Although the ESA prohibits actions that directly harm listed animals and, to a lesser extent, listed plants, it does not require landowners to take affirmative actions to maintain or restore habitats for listed species. Thus, a landowner is under no obligation to control exotic weeds, undertake a program of prescribed burning, or do any of the other things that may be absolutely necessary for the long-term survival of many imperiled species. In fact, it may be possible for a landowner to rid himself of an endangered species "problem" by literally doing nothing and waiting until the habitat is no longer suitable for the species in question. Even those landowners who care deeply about endangered species and wish to protect them face a daunting burden: The costs of undertaking these management actions can be considerable and, at present, are usually not tax deductible.

With a growing list of species in need of attention and less money to spend per species (Wilcove et al. 1996), the USFWS cannot hope to cover the necessary management costs for most of the plants and animals it aspires to protect. Nor can it count on the goodwill of landowners to contribute their own money or labor for actions they are not obligated to perform and that ultimately may result in restrictions on the use of their property. As a nation, therefore, we are incurring a growing "management debt" associated with efforts to protect imperiled species. To address this problem, it will be necessary to supplement the regulatory controls of the ESA and other wildlife protection laws with a wide array of incentives to reward landowners who wish to manage their property to benefit endangered species (Wilcove et al. 1996). Without such incentives, the United States stands to lose a large proportion of its imperiled plants and animals.

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