Environmental and Economic Costs of Nonindigenous Species in the United States

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Approximately 50,000 nonindigenous (non-native) species are estimated to have been introduced to the United States. Some of these are beneficial; for example, species introduced as food crops (e.g., corn, wheat, and rice) and as livestock (e.g., cattle and poultry) now provide more than 98% of the US food system, at a value of approximately $800 billion per year (USBC 1998). Other exotic species have been introduced for landscape restoration, biological pest control, sport, pets, and food processing, also with significant benefits. Some nonindigenous species, however, have caused major economic losses in agriculture, forestry, and several other segments of the US economy, in addition to harming the environment. One study reported that 79 exotic species had caused approximately $97 billion in damages during the period 1906–1991 (OTA 1993).

Estimating the full extent of the environmental damage caused by exotic species and the number of species extinctions they have caused is difficult because little is known about the estimated 750,000 species in the United States, half of which have not even been described (Raven and Johnson 1992). Nevertheless, approximately 400 of the 958 species that are listed as threatened or endangered under the Endangered Species Act are considered to be at risk primarily because of competition with and predation by nonindigenous species (TNC 1996, Wilcove et al. 1998). In other regions of the world, as many as 80% of the endangered species are threatened due to the pressures of non-native species (Armstrong 1995). Many other species worldwide, even if they do not have endangered status, are also negatively affected by alien species or ecosystem changes caused by alien species.

Estimating the economic impacts that are associated with nonindigenous species is also difficult; nevertheless, enough data are available to quantify some of the impacts on agriculture, forestry, and public health in the United States. In this article, we assess the magnitude of the environmental impacts and economic costs associated with the diverse nonindigenous species that have become established within the United States. Although species translocated within the United States can also have significant impacts, our assessment is limited to nonindigenous species that did not originate within the United States or its territories.

THE APPROXIMATELY 50,000 NONINDIGENOUS SPECIES IN THE UNITED STATES CAUSE MAJOR ENVIRONMENTAL DAMAGE AND LOSSES TOTALING APPROXIMATELY $137 BILLION PER YEAR

Environmental damages and associated control costs

Most plant and vertebrate animal introductions have been intentional, whereas most invertebrate animal and microbe introductions have been accidental. In the past 40 years, the rate of introductions and risks associated with biotic invaders have increased enormously because of human population growth, rapid movement of people, and alteration of the environment. In addition, more goods and materials are being traded among nations than ever before, creating increased opportunities for unintentional introductions (Bryan 1996, USBC 1998).

Some of the approximately 50,000 species of plants, animals, and microbes that have invaded the United States cause many different types of damage to managed and natural ecosystems (Table 1). Several examples reveal the extent of these damages and control costs.

Plants. Most alien plants now established in the United States were introduced for food, fiber, or ornamental purposes. An estimated 5000 introduced plant species have escaped and now exist in US natural ecosystems (Morse et al. 1995), compared with a total of approximately 17,000 species of native plants (Morin 1995). In Florida, of the approximately 25,000 alien plant species (imported mainly as ornamentals for cultivation), more than 900 have

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Type of organism	Losses and damages (x $1 million)	Control costs (x $1 million)	Total costs (x $1 million)
Plants			
Purple loosestrife	NA[a]	45	45
Aquatic weeds	10	100	110
Melaleuca tree	NA	3–6	3–6
Crop weeds	23,400	3,000	26,400
Weeds in pastures	1,000	5,000	6,000
Weeds in lawns, gardens, golf courses	NA	1,500	1,500
Mammals			
Wild horses and burros	5	NA	5
Feral pigs	800	0.5	800.5
Mongooses	50	NA	50
Rats	19,000	NA	19,000
Cats	17,000	NA	17,000
Dogs	250	NA	250
Birds			
Pigeons	1,100	NA	1,100
Starlings	800	NA	800
Reptiles and amphibians			
Brown tree snake	1	4.6	5.6
Fishes	1,000	NA	1,000
Arthropods			
Imported fire ant	600	400	1,000
Formosan termite	1,000	NA	1,000
Green crab	44	NA	44
Gypsy moth	NA	11	11
Crop pests	13,900	500	14,400
Pests in lawns, gardens, golf courses	NA	1,500	1,500
Forest pests	2,100	NA	2,100
Mollusks			
Zebra mussel	NA	NA	100
Asian clam	1,000	NA	1,000
Shipworm	205	NA	205
Microbes			
Crop plant pathogens	21,000	500	21,500
Plant pathogens in lawns, gardens, golf courses	NA	2,000	2,000
Forest plant pathogens	2,100	NA	2,100
Dutch elm disease	NA	100	100
Livestock diseases	9,000	NA	9,000
Human diseases	NA	6,500	6,500
All organisms			136,630

[a]NA, not available.

Table 1. Estimated annual costs associated with some nonindigenous species introduced to the United States, in millions of dollars (see text for details and sources).

escaped and become established in surrounding natural ecosystems (Frank and McCoy 1995a, Frank et al. 1997, Simberloff et al. 1997). More than 3000 plant species have been introduced into California, and many of these have escaped into the natural ecosystem as well (Dowell and Krass 1992).

Some of the nonindigenous plants that have become established in the United States have displaced several native plant species (Morse et al. 1995). Nonindigenous weeds are spreading and invading approximately 700,000 hectares of US wildlife habitat per year (Babbitt 1998). For example, the European purple loosestrife (*Lythrum salicaria*), which was introduced in the early nineteenth century as an ornamental plant (Malecki et al. 1993), has been spreading at a rate of 115,000 hectares per year and is changing the basic structure of most of the wetlands it has invaded (Thompson et al. 1987). Competitive stands of purple loosestrife have reduced the biomass of 44 native plants and endangered wildlife, including the bog turtle (*Clemmys muhlenbengil*) and several duck species, that depend on these native plants (Gaudet and Keddy 1988). Loosestrife now occurs in 48 states and costs $45 million per year in control costs and forage losses (ATTRA 1997).

Many introduced plant species established in the wild are having an effect on federal lands (Hiebert and Stubbendieck 1993). In Great Smoky Mountains National Park, for example, 400 of the approximately 1500 vascular plant species are exotic, and 10 of these are currently displacing and threatening native plant species (Hiebert and Stubbendieck 1993). The problem of introduced plants is especially significant in Hawaii, where 946 of the 2690 plant species are nonindigenous (Eldredge and Miller 1997).

Sometimes, one nonindigenous plant species competitively overruns an entire ecosystem. For example, in California, yellow star thistle (*Centaurea solstitalis*) now dominates more than 4 million hectares of northern California grassland, resulting in the total loss of this once productive grassland (Campbell 1994). Similarly, European cheatgrass (*Bromus tectorum*) is dramatically changing the vegetation and fauna of many natural ecosystems. This annual grass has invaded and spread throughout the shrub–steppe habitat of the Great Basin in Idaho and Utah, predisposing the invaded habitat to fires (Kurdila 1995, Vitousek et al. 1996, 1997). Before the invasion of cheatgrass, fire burned once every 60–110 years and shrubs had a chance to become well established. Now, the occurrence of fires every 3–5 years has led to a decrease in shrubs and other vegetation and to the occurrence of competitive monocultures of cheatgrass on 5 million hectares in Idaho and Utah (Whisenant 1990). The animals dependent on the shrubs and other original vegetation have been reduced or eliminated.

An estimated 138 nonindigenous tree and shrub species have invaded native US forest and shrub ecosystems (Campbell 1998). Introduced trees include salt cedar (*Tamarix pendantra*), eucalyptus (*Eucalyptus* spp.), Brazilian pepper (*Schinus terebinthifolius*), and Australian melaleuca (*Melaleuca quenquenervia*; OTA 1993, Miller 1995, Randall 1996). Some of these trees have displaced native trees, shrubs, and other vegetation types, and populations of some associated native animal species have been reduced in turn (OTA 1993). For example, the melaleuca tree is spreading at a rate of 11,000 hectares per year throughout the vast forest and grassland ecosystems of the Florida Everglades (Campbell 1994), where it damages the natural vegetation and wildlife (OTA 1993).

Exotic aquatic weeds are also a significant problem in the United States. For example, in the Hudson River basin of New York, there are 53 exotic aquatic weed species (Mills et al. 1997). In Florida, exotic aquatic plants, including hydrilla (*Hydrilla verticillata*), water hyacinth (*Eichhornia crassipes*), and water lettuce (*Pistia straiotes*), are altering fish and other aquatic animal species, choking waterways, changing nutrient cycles, and reducing recreational use of rivers and lakes. Active control measures of aquatic weeds have become necessary (OTA 1993). For instance, Florida spends approximately $14.5 million each year on hydrilla control (Center et al. 1997). Despite this expenditure, hydrilla infestations in just two Florida lakes have cost an estimated $10 million per year in recreational losses (Center et al. 1997). In the United States as a whole, a total of $100 million is invested annually in control of nonindigenous aquatic weed species (OTA 1993).

Mammals. Approximately 20 mammal species have been introduced into the United States, among them dogs, cats, horses, burros, cattle, sheep, pigs, goats, and deer (Layne 1997). Several of these species escaped or were released into the wild and have become pests by preying on native animals, grazing on vegetation, or intensifying soil erosion. For example, goats (*Capra hirus*) introduced on San Clemente Island, California, have caused the extinction of eight endemic plant species and the endangerment of eight others (Kurdila 1995).

Many small mammals, especially rodents, have been introduced into the United States. Introduced rodent species include the European (black or tree) rat (*Rattus rattus*), the Asiatic (Norway or brown) rat (*Rattus norvegicus*), the house mouse (*Mus musculus*), and the European rabbit (*Oryctolagus cuniculus*; Layne 1997). Some introduced rodents have become serious pests on farms, in industries, and in homes (Layne 1997). Rats and mice are particularly abundant and destructive on farms. On poultry farms, there is approximately one rat per five chickens (Smith 1984, David Pimentel, unpublished data). Using this ratio, the total rat population on US poultry farms would easily number more than 1.4 billion (USDA 1998). Assuming that the number of rats per chicken has declined because of improved rat control since these observations were made, we estimate that the number of rats on poultry and other farms is approximately 1 billion. With an estimated additional 250 million rats in urban areas (Wachtel and McNeely 1985), there are an estimated 1.25 billion rats in the United States (USBC 1998). If we assume, conservatively, that each adult rat consumes or destroys stored grains (Chopra 1992, Ahmed et al. 1995) and other materials valued at $15 per year, then the total cost of destruction by introduced rats in the United States is approximately $19 billion per year. In addition, rats cause fires (by gnawing electric wires), pollute foodstuffs, and act as vectors of several diseases, including salmonellosis, leptospirosis, and, to a lesser degree, plague and murine typhus (Richards 1989). They also prey on some native invertebrate and vertebrate species, including birds and bird eggs (Amarasekare 1993).

The Indian mongoose (*Herpestes auropunctatus*) is yet another exotic mammal that has caused extensive damage. One of the first cases of the failure of biological control, the mongoose was first introduced into Jamaica in 1872 for biological control of rats in sugarcane (Pimentel 1955). It was subsequently introduced to Puerto Rico, other West Indian Islands, and Hawaii for the same purpose. The mongoose controlled the Asiatic rat but not the European rat, and it preyed heavily on native ground-nesting birds (Pimentel 1955, Vilella and Zwank 1993). It also preyed on beneficial native amphibians and reptiles, causing at least seven amphibian and reptile extinctions in Puerto Rico and other islands of the West Indies (Henderson 1992). In addition, the mongoose emerged as the major vector and reservoir of rabies and leptospirosis in Puerto Rico and other islands (Everard and Everard 1992). Based on public health damages, poultry deaths in Puerto Rico and Hawaii, extinctions of amphibians and reptiles, and destruction of native birds, we estimate that the mongoose is causing approximately $50 million in damages each year in Puerto Rico and the Hawaiian Islands (Rodolfo Zuniga, personal observation; David Pimental, unpublished data).

Introduced cats have also become a serious threat to some native birds and other animals. There are an estimated 63 million pet cats in the United States (Nassar and Mosier 1991) and as many as 30 million feral cats (Luoma 1997). Winter (1999) estimated that 35% of pet cats never go outside and, therefore, do not prey on birds and other animals. Outdoor pet cats and feral cats prey on native birds (Fitzgerald 1990), small native mammals, amphibians, and reptiles (Dunn and Tessaglia 1994). Winter (1999) reported that feral cats in Wisconsin kill from 7.8 million to 217 million birds each year. Based on an estimated 600,000 feral cats in Wisconsin, these data suggest that feral cats kill at least 13 birds per cat per year. McKay (1996) estimated that eight birds are killed per feral cat and outdoor pet cat each year. Based on McKay's more conservative estimate, and with a total of 71 million feral and outdoor pet cats, we estimate that cats kill approximately 568 million birds per year in the United States.

Although it is not easy to determine the value of each bird killed, a reasonable value might be $30. This cost is based on the facts that a bird watcher spends $0.40 per bird observed (USFWS 1988), a hunter spends $216 per bird shot (USFWS 1988), and ornithologists spend $800 per bird reared for release (Tinney 1981). Another way to look at the value of each bird is by considering that EPA fines polluters $10 per fish killed, including small, immature fish (Pimentel and Greiner 1997); a value of $30 per bird therefore seems roughly equivalent. Based on this value, the total damage to the US bird population is approximately $17 billion per year. This figure does not include the value of the small mammals, amphibians, and reptiles that are killed by feral and pet cats (Dunn and Tessaglia 1994).

Like cats, most dogs introduced to the United States were introduced as domestic animals, but some have escaped into the wild. Many of these wild dogs run in packs and kill deer, rabbits, cattle, sheep, and goats. Carter (1990) reported that feral dog packs in Texas cause more than $5 million in livestock losses each year. Dog packs have also become a serious problem in Florida (Layne 1997). In addition to the damages caused by dogs in Texas, and conservatively assuming $5 million for all damages for the other 49 states combined, total losses in livestock killed by dogs is approximately $10 million per year.

Moreover, an estimated 4.7 million people are bitten by feral and pet dogs annually, with 800,000 cases requiring medical treatment (Sacks et al. 1996). The Centers for Disease Control estimates that medical treatment for dog bites costs $165 million per year, with indirect costs, such as lost work, increasing the total costs of dog bites to $250 million per year (Colburn 1999, Quinlan and Sacks 1999). In addition, dog attacks cause 11–14 deaths per year, and 80% of the victims are small children (CDC 1997).

Birds. Approximately 97 of the 1000 bird species in the United States are exotic (Temple 1992). Only approximately 5% of the introduced bird species (e.g., chickens) are considered beneficial; 56% are considered pests (Temple 1992). Pest species include the pigeon, which was introduced into the United States for agricultural purposes.

Introduced bird species are an especially severe problem in Hawaii. Of the 69 nonindigenous bird species introduced to Hawaii between 1850 and 1984, 35 are still extant on the islands (Moulton and Pimm 1983, Pimm 1991). One such species, the common myna (*Acridotheres tristis*), was introduced in 1865 to help control pest cutworms and armyworms in sugarcane (Kurdila 1995). However, it became the major disperser of seeds of an introduced harmful weed, *Lantana camara*.

The English, or house, sparrow (*Passer domesticus*) was introduced to the continental United States in 1853 to control the canker worm (Laycock 1966, Roots 1976). By 1900, English sparrows had become pests because they damage plants around homes and public buildings and consume wheat, corn, and the buds of fruit trees (Laycock 1966). Furthermore, they harass native birds, including robins, Baltimore orioles, and yellow-billed and black-billed cuckoos, and they displace native bluebirds, wrens, purple martins, and cliff swallows from their nesting sites (Laycock 1966, Roots 1976, Long 1981). They are also associated with the spread of approximately 30 human and livestock diseases (Weber 1979).

The single most serious pest bird in the United States is the exotic common pigeon (*Columba livia*), which exists in most cities of the world (Robbins 1995). Pigeons are considered a nuisance because they foul buildings, statues, cars, and sometimes people, and they feed on grain (Long 1981, Smith 1992). The control costs for pigeons are at least $9 per pigeon per year (Haag-Wackernagel 1995). Assuming that there is one pigeon per hectare in urban areas (Johnston and Janiga 1995), or approximately 0.5 pigeons per person, and using potential control costs as a surrogate for losses, pigeons cause $1.1 billion per year in damages. These control costs do not include the environmental damages associated with pigeons, which serve as reservoirs and vectors for over 50 human and livestock diseases, including parrot fever, ornithosis, histoplasmosis, and encephalitis (Weber 1979, Long 1981).

Amphibians and reptiles. Approximately 53 amphibian and reptile species have been introduced into the United States. All of these nonindigenous species occur in relatively warm states—for example, Florida is now host to 30 species and Hawaii to 12 (McCoid and Kleberg 1995, Lafferty and Page 1997). The negative ecological impacts of several of these exotic species have been enormous.

The brown tree snake (*Boiga irregularis*) was accidentally introduced to the snake-free US territory of Guam immediately after World War II, when military equipment was moved onto Guam (Fritts and Rodda 1995). The snake population soon reached densities of 100 snakes per hectare and dramatically reduced populations of native birds, mammals, and lizards. Of the 13 species of native forest birds originally found on Guam, only three still exist, and of the 12 native species of lizards, only three have survived (Rodda et al. 1997). The brown tree snake eats chickens, eggs, and caged birds, causing major problems to small farmers and pet owners. It also crawls up trees and utility poles and has caused power outages on the island, one of which cost the power utility more than $250,000 (Teodosio 1987). Local outages that affect businesses are estimated to cost $2000–10,000 per commercial customer (Coulehan 1987). With approximately 86 outages per year (BTSCC 1996), our conservative estimate of the cost of brown tree snake–related power outages is $1 million per year. In addition, the brown tree snake is slightly venomous and has caused public health problems, especially when it has bitten children. At one hospital emergency room on Guam, approximately 26 people per year are treated for snake bites (OTA 1993). Some bitten infants require hospitalization and intensive care, at an estimated total cost of $25,000 per year (Thomas Fritts, US Geological Survey, personal communication).

The total costs of endangered species recovery efforts, environmental planning related to snake containment on Guam, and other programs directly stemming from the snake's invasion of Guam reach more than $1 million per year; in addition, up to $2 million per year is invested in research to control this serious pest (Thomas Fritts, US Geological Survey, personal communication). The brown tree snake has also invaded Hawaii but thus far has been exterminated. Hawaii's concern about the snake, however, has prompted the federal government to invest $1.6 million per year in brown tree snake control (Holt 1997–1998). The total cost associated with this snake is therefore more than $5.6 million per year.

Fish. A total of 138 nonindigenous fish species has been introduced into the United States (Courtenay et al. 1991, Courtenay 1993, 1997). Most of these introduced fishes have been established in states with mild climates, such as Florida (50 species; Courtenay 1997) and California (56 species; Dill and Cordone 1997). In Hawaii, 33 nonindigenous freshwater fish species have become established (Maciolek 1984).

Introduced fish species frequently alter the ecology of aquatic ecosystems. For instance, the grass carp (*Ctenopharyngodon idella*) reduces natural aquatic vegetation, and the common carp (*Cyprinus carpio*) reduces water quality by increasing turbidity. These changes have caused the extinctions of some native fish species (Taylor et al. 1984). Forty-four fish species native to the United States are threatened or endangered by nonindigenous fish species (Wilcove and Bean 1994). An additional 27 native fish species have been harmed by introductions (Wilcove and Bean 1994).

Although nonindigenous fish species have reduced the numbers of some native fish species, driven others to extinction, and hybridized with still others, alien fish do provide some economic benefits in the improvement of sport fishing. Sport fishing contributes $38 billion annually to the US economy (Bjergo et al. 1995, USBC 1998). However, even taking into account these economic benefits, based on the more than 40 nonindigenous species that have negatively affected native fishes and other aquatic biota, a conservative estimate puts the economic losses due to exotic fish at more than $1 billion annually (Walter R. Courtenay, Florida Atlantic University, personal communication).

Arthropods. Approximately 4500 arthropod species (more than 2500 species in Hawaii and more than 2000 in the continental United States) and nearly 100 aquatic invertebrate species have been introduced to the United States (OTA 1993). Approximately 95% of these introductions were accidental, with many species gaining entrance via contaminated plants or through soil and water ballast from ships.

Some accidentally introduced arthropods have caused extensive damage to forests. For example, the balsam woolly adelgid (*Adelges piceae*) inflicts severe damage in balsam-fir natural forest ecosystems (Jenkins 1998). According to Alsop and Laughlin (1991), this aphid is destroying the old-growth spruce–fir forest in many regions. Over the last two decades, it has spread throughout the southern Appalachians, where it has destroyed up to 90% of the fraser firs (Howard S. Neufeld, Appalachian State University, personal communication). Adelgid-mediated forest death has led to the loss of two native bird species and the invasion of three other bird species (Alsop and Laughlin 1991).

Other introduced insect species have become pests of livestock and wildlife. For example, the imported red fire ant (*Solenopsis invicta*) kills poultry chicks, lizards, snakes, and ground-nesting birds (Vinson 1994). Allen et al. (1995) reported that the ants had caused a 34% decrease in swallow nesting success as well as a decline in northern bobwhite quail populations. The estimated damages to livestock, wildlife, and public health caused by fire ants in Texas is estimated to be $300 million per year. An additional $200 million is invested in control per year (Vinson 1992, TAES 1998). Assuming similar damages in other infested southern states—including Florida, Georgia, and Louisiana—fire ant damages total more than $1 billion per year. Southern states are also affected by another insect, the Formosan termite (*Coptotermes formosanus*), which causes structural damages totaling approximately $1 billion per year in the southern United States, especially the New Orleans region (Corn et al. 1999).

Insects are not the only costly arthropod invaders. The European green crab (*Carcinus maenas*), which was introduced as a food source, has been associated with the demise of the softshell clam industry in New England and the maritime provinces of Canada (Lafferty and Kuris 1996). It also destroys commercial shellfish beds and preys on large numbers of native oysters and crabs, with an annual estimated economic impact of $44 million per year (Lafferty and Kuris 1996).

Mollusks. Eighty-eight species of mollusks have been introduced, both intentionally and accidentally, and become established in US aquatic ecosystems (OTA 1993). Two have become serious pests: the zebra mussel (*Dreissena polymorpha*) and the Asian clam (*Corbicula fluminea*).

The zebra mussel was first found in Lake St. Clair, in Michigan, after gaining entrance via ballast water released in the Great Lakes from ships that had traveled from Europe (Benson and Boydstun 1995). It has spread to most of the aquatic ecosystems in the eastern United States, reaching densities of 700,000/m^2 in some locations (Griffiths et al. 1991), and is expected to invade most freshwater habitats throughout the nation in approximately 20 years (Benson and Boydstun 1995). Large zebra mussel populations not only reduce food and oxygen for native fauna but also have been observed completely covering native mussels, clams, and snails, thereby further threatening their survival (Benson and Boydstun 1995, Keniry and Marsden 1995). Zebra mussels also invade and clog water intake pipes and water filtration and electric generating plants; Charles R. O'Neill (New York Sea Grant, personal communication) estimated that they will cause $100 million per year in damages to these facilities and associated control costs.

Although the Asian clam grows and disperses less rapidly than the zebra mussel, it too is causing significant fouling problems and threatening native species. Costs associated with its fouling damage are approximately $1 billion per year (Isom 1986, OTA 1993). Another pest mollusk is the introduced shipworm (*Teredo navalis*), which was first introduced into the San Francisco Bay via wooden ships. It has caused serious damage to wood docks since the early 1990s. Currently, damages to docks and ships are estimated to be approximately $200 million per year (Cohen and Carlton 1995).

Crop, pasture, and forest losses and associated control costs

Many weeds, pest insects, and plant pathogens are biological invaders. These nonindigenous species cause several billion dollars worth of losses to US crops, pastures, and forests annually. In addition, several billion dollars are spent on pest control.

Weeds. In crop systems, including forage crops, an estimated 500 introduced plant species have become weed pests; some of these, such as Johnson grass (*Sorghum halepense*) and kudzu (*Pueraria lobata*), were actually introduced as crops and then became pests (Pimentel et al. 1989). Most other weeds were accidentally introduced with crop seeds, soil used as ballast, or various imported plant materials. Two of the most costly accidentally introduced weeds are yellow rocket (*Barbarea vulgaris*) and Canada thistle (*Cirsium arvense*).

In US agriculture, weeds cause an overall reduction of 12% in crop yields, which represents approximately $32 billion in lost crop production annually, based on the crop potential value of all US crops of more than $267 billion per year (USBC 1998). Based on a survey that found that approximately 73% of the weed species are nonindigenous (Pimentel 1993), it follows that approximately $23.4 billion per year of these crop losses are due to introduced weeds. However, nonindigenous weeds are often more serious pests than native weeds; thus, the estimate of $23.4 billion per year is conservative. In addition to direct losses, approximately $4 billion is spent each year on herbicides that are applied to US crops (Pimentel 1997); approximately $3 billion is used for control of nonindigenous weeds. Therefore, the total annual cost of introduced weeds to the US agricultural economy is approximately $26.4 billion.

It is important to note that in making this calculation, we simply calculated the proportion of potential losses caused by nonindigenous weeds based on the percentage of weed species that were nonindigenous. We recognize that if there were no nonindigenous weeds in crops, native weeds would replace them, and one way to assess the losses caused by nonindigenous weeds would therefore have been to assess the increase in losses caused by nonindigenous weeds above those caused by native weeds. The literature confirms that nonindigenous weeds are a greater problem than native weeds, but the quantitative increase in losses is not documented. Even though our approach does not take into account the fact that native weeds would partially substitute for exotic weeds, any potential overestimation of the impact of exotic weeds would be cancelled out by the fact that the cost figure did not include other potential losses caused by nonindigenous weeds. For example, we did not include the approximately $9 billion in environmental and public health damages caused by the large quantities of herbicides and other pesticides used to control exotic weeds and other pests each year in the United States (Pimentel and Greiner 1997). We also did not take into account the effect of exotic weeds on food prices. For every 1% decrease in crop yield, on average, there is a 4.5% increase in crop price value at the farm gate (Pimentel 1997). Consequently, because nonindigenous weeds cause more extensive crop losses than native weeds, they cause a greater increase in the cost of food.

Weeds, both native and exotic, are also a problem in pastures, where 45% of weed species are nonindigenous (Pimentel 1993). US pastures provide approximately $10 billion in forage crops annually (USDA 1998), and the estimated losses due to inedible weeds are approximately $2 billion (Pimentel 1991). Forage losses due to nonindigenous weeds therefore amount to nearly $1 billion per year. Some introduced weeds, such as leafy spurge (*Euphoria esula*), are toxic to cattle and wild ungulates (Trammel and Butler 1995). In addition, several nonindigenous thistles have reduced native forage plant species in pastures, rangelands, and forests, thus reducing cattle grazing (Dewey 1991). According to Interior Secretary Bruce Babbitt, ranchers spend approximately $5 billion each year to control invasive nonindigenous weeds in pastures and rangelands; nevertheless, these weeds continue to spread (Babbitt 1998).

Control of weed species in lawns, gardens, and golf courses makes up a significant proportion of the total management costs for lawns, gardens, and golf courses of approximately $36 billion per year (USBC 1998). In fact, Templeton et al. (1998) estimated that each year, approximately $1.3 billion of the $36 billion is spent just on residential weed, insect, and disease pest control. Because a large proportion of the residential weeds, such as dandelions (*Taraxacum officinale*), are exotics, we estimate that $500 million is spent to control exotic weeds in residential areas and an additional $1 billion is spent to control nonindigenous weeds on golf courses. Weed trees also have an economic impact. For instance, $3–6 million per year is being spent in efforts to control the melaleuca tree in Florida (Curtis J. Richardson, Duke University, personal communication).

Vertebrate pests. Horses (*Equus caballus*) and burros (*Equus asinus*), which were introduced around 1750 in the western United States (some were deliberately released on rangelands, and a few escaped), have attained wild populations of approximately 50,000 animals (Pogacnik 1995). These animals graze heavily on native vegetation, allowing nonindigenous annuals to displace native perennials (Rosentreter 1994). Burros inhabiting the northwestern United States also diminish the primary food sources of native bighorn sheep and seed-eating birds, thereby reducing the abundance of these native animals (Kurdila 1995). In total, the large populations of introduced wild horses and burros cost the nation an estimated $5 million per year in forage losses (David Pimentel, Lori Lach, Rodolfo Zuniga, Doug Morrison, unpublished data).

Feral pigs (*Sus scrofa*), which are native to Eurasia and North Africa, have been introduced into some US parks for hunting, including parks in the California coastal prairie and in the Hawaiian islands, whose vegetation they have changed substantially (Kotanen 1995). In Hawaii, more than 80% of the soil in regions inhabited by pigs is bare (Kurdila 1995). This disturbance allows annual plants to invade the overturned soil, intensifying soil erosion. Pig control in the three Hawaiian national parks costs approximately $100 per pig per year (Rodolfo Zuniga, unpublished data); each park contains approximately 1500 pigs (Stone et al. 1992), so the total pig control costs are approximately $450,000 per year.

Feral pigs have also become a serious problem in Florida, where their numbers have risen to more than 500,000 (Layne 1997); similarly, in Texas they number 1–1.5 million (Joel P. Bach, Texas A&M University, personal communication). Nationwide, there are an estimated 4 million feral pigs. In Florida, Texas, and other southern states, feral pigs damage grain, peanut, soybean, cotton, hay, and various vegetable crops as well as the environment (Rollins 1998). Feral pigs also transmit serious human and livestock diseases, including brucellosis, pseudobrucellosis, and trichinosis (Davis 1998). Based on environmental and crop damages of approximately $200 per pig annually (indeed, one pig can cause up to $1000 of damage to crops in one night; Joel P. Bach, Texas A&M University, personal communication), the yearly damage caused by the 4 million feral pigs in the United States amounts to approximately $800 million. This estimate is conservative because pigs cause significant environmental damages and diseases that cannot easily be translated into dollar values.

Other exotic animals that threaten crop production include birds. European starlings (*Sturnus vulgaris*), which are estimated to occur at densities of more than one per hectare in agricultural regions (Moore 1980), are capable of destroying as much as $2000 worth of cherries per hectare (Feare 1980). In grain fields, starlings consume approximately $6 worth of grain per hectare (Feare 1980). Conservatively assuming that starlings cause $5 in crop losses per hectare of US cropland, the total loss due to starlings would be approximately $800 million per year. In addition, these aggressive birds have displaced numerous native birds (Laycock 1966). Starlings have also been implicated in the transmission of 25 diseases, including parrot fever and several other human diseases (Laycock 1966, Weber 1979).

Insect and mite pests. Approximately 1000 nonindigenous insect and mite species are crop pests in the United States. Hawaii has 5246 identified native insect species and an additional 2582 introduced insect species (Howarth 1990, Frank and McCoy 1995a, Eldredge and Miller 1997). Introduced insects account for 98% of the crop pest insects in Hawaii (Beardsley 1991). In California, the 600 introduced species are responsible for 67% of all crop losses (Dowell and Krass 1992).

Each year, pest insects destroy approximately 13% of potential US crop production, which represents a value of approximately $34.7 billion (USBC 1998). Considering that approximately 40% of the pests were introduced (Pimentel 1993), we estimate that introduced pests cause approximately $13.9 billion in US crop losses each year. This estimate is conservative because we did not factor in the environmental costs of using insecticides and miticides or any of the increased crop losses that these exotic pests may cause. In addition, approximately $1.2 billion worth of pesticides are applied for control of all crop insects each year in the United States (Pimentel 1997). The portion applied against introduced pest insects is approximately $500 million per year. Therefore, the total cost for introduced nonindigenous insect pests is approximately $14.4 billion per year. In addition, based on our analysis of the management costs of lawns, gardens, and golf courses, we estimate that control costs of pest insects and mites in lawns, gardens, and golf courses are at least $1.5 billion per year (residential is estimated to be $500 million, and golf courses are estimated to be $1 billion).

Nonindigenous insect species have invaded US forests as well as croplands. Of the approximately 360 nonindigenous insect species that have become established in American forests (Liebold et al. 1995), 30% are now serious pests (Elizabeth P. Harausz, David Pimentel, unpublished data). Insects cause the loss of approximately 9% of forest products, such as lumber and pulp wood, amounting to a cost of $7 billion per year (Hall and Moody 1994, USBC 1998). Because 30% of the pests are nonindigenous, annual forest losses attributed to nonindigenous insect species total approximately $2.1 billion per year.

One particularly devastating exotic insect is the gypsy moth (*Lymantria dispar*), which was intentionally introduced into Massachusetts in the 1800s for possible silk production. The gypsy moth has developed into a major pest of US forest and ornamental trees, especially oaks (Campbell and Schlarbaum 1994). The US Forest Service currently spends approximately $11 million annually on gypsy moth control (Campbell and Schlarbaum 1994).

Plant pathogens. There are an estimated 50,000 parasitic and nonparasitic diseases of plants in the United States, most of which are caused by fungi (USDA 1960). In addition, more than 1300 species of viruses are plant pests in the United States (USDA 1960). Many of these microbes are non-native and were introduced inadvertently with seeds and other parts of host plants (that were themselves introduced deliberately) and have become major crop pests (Pimentel 1993). Including the introduced plant pathogens plus other soil microbes, we estimate conservatively that more than 20,000 species of microbes have invaded the United States.

US crop losses to all plant pathogens total approximately $33 billion per year (Pimentel 1997, USBC 1998). Approximately 65% (Pimentel 1993), or $21 billion, of the losses are attributable to nonindigenous plant pathogens. In addition, growers spend $720 million each year on fungicides (Pimentel 1997), approximately $500 million of which is used to combat nonindigenous plant pathogens specifically. The total damage and control costs of nonindigenous plant pathogens therefore amount to approximately $21.5 billion per year. In addition, we estimate, based on the fact that 65% of plant pathogens are exotic, that control costs of plant pathogens in lawns, gardens, and golf courses are at least $2 billion per year (David Pimentel, Lori Lach, Rodolfo Zuniga, Doug Morrison, unpublished data).

In US forests, more than 20 nonindigenous species of plant pathogens attack woody plants (Liebold et al. 1995). Two of the most serious plant pathogens are the chestnut blight fungus (*Cryphonectria parasitica*) and Dutch elm disease (*Ophiostoma ulmi*). Before the accidental introduction of chestnut blight, approximately 25% of eastern US deciduous forest consisted of American chestnut trees (Campbell 1994). Now, the American chestnut has all but disappeared. Removal of elm trees devastated by *O. ulmi* costs approximately $100 million per year (Campbell and Schlarbaum 1994).

In addition, plant pathogens of forest plants cause the loss of approximately 9%, or $7 billion worth, of forest products each year (Hall and Moody 1994, USBC 1998). The proportion of introduced plant pathogens in forests is similar to that of introduced insects (approximately 30%); thus, approximately $2.1 billion in forest products are lost each year to nonindigenous plant pathogens in the United States. Again, damages from exotic pests appear to be more severe than those from native pests.

Livestock pests

Just as alien pests were introduced along with non-native crop plants, exotic microbes (e.g., calf diarrhea rotavirus) and parasites (e.g., face flies, *Musca autumnalis*) were introduced along with livestock brought to the United States (Drummond et al. 1981, Morgan 1981). In addition to the hundreds of pest microbes and parasites that have already been introduced, more than 60 microbes and parasites could invade from other regions of the globe and become serious pests to US livestock (USAHA 1984). A conservative estimate of the losses to US livestock from exotic microbes and parasites was reported to be approximately $3 billion per year in 1980 (Drummond et al. 1981, Morgan 1981). Current livestock losses to pests are estimated to be approximately $9 billion per year (Kelsey Hart, Cornell University, personal communication).

Human diseases

An increasing threat of exotic diseases exists because of rapid transportation, encroachment of civilization into new ecosystems, and growing environmental degradation. The nonindigenous diseases now having the greatest impact on humans in the United States are AIDS, syphilis, and influenza (Newton-John 1985, David Pimentel, Lori Lach, Rodolfo Zuniga, Doug Morrison, unpublished data). In 1996, there were 106,005 cases of AIDS, with

39,200 deaths (USBC 1998). The total US health care cost for the treatment of AIDS averages approximately $6 billion per year (USPHS 1994).

New influenza strains originating in the Far East spread quickly to the United States. Influenza causes 540 deaths in the United States each year (USBC 1998). Costs of hospitalizations for a single outbreak of influenza, such as type A, can exceed $300 million per year (Chapman et al. 1992). In addition, each year there are approximately 53,000 cases of syphilis in the United States; treatment of newborn children infected with syphilis costs $18.4 million per year (Bateman et al. 1997). In total, annual US treatment costs for these diseases are approximately $6.5 billion. In addition, AIDS and influenza take the lives of more than 40,000 people each year in the United States. The costs of treating other exotic diseases push the total costs of exotic disease much higher.

The nonindigenous species threat

With more than 50,000 nonindigenous species in the United States, the fraction that is harmful does not have to be large to inflict significant damage to natural and managed ecosystems and cause public health problems. A suite of ecological factors may cause particular nonindigenous species to become abundant and persistent. These include the lack of controlling natural enemies (e.g., purple loosestrife and imported fire ant), the ability of an alien parasite to switch to a new host (e.g., AIDS virus in humans and gypsy moth in US oaks), an ability to be an effective predator in the new ecosystem (e.g., brown tree snake and feral cats), the availability of artificial or disturbed habitats that provide a highly invadable ecosystem for the aliens (e.g., weeds in crop and lawn habitats), and high adaptability to novel conditions (e.g., water hyacinth and zebra mussel).

The analysis presented in this article reveals that economic damages associated with nonindigenous species effects and their control amount to approximately $137 billion per year (Table 1). The Office of Technology Assessment (OTA 1993) reported average costs of $1.1 billion per year ($97 billion over 85 years) for 79 species. Our higher estimate reflects the fact that we included more than 10 times the number of species in our assessment and found higher costs reported in the literature than OTA (1993) for some of the same species. For example, for the zebra mussel, OTA reported damages and control costs of slightly more that $300,000 per year, whereas an updated estimate is $100 million per year (Charles R. O'Neill, New York Sea Grant, personal communication).

Although we reported a specific total for economic damages and associated control costs resulting from invasive nonindegenous species, precise economic costs associated with some of the most ecologically damaging exotic species are not available. The brown tree snake, for example, has been responsible for the extinction of dozens of bird and lizard species on Guam. Yet for this snake, only minimal cost data are known. In other cases, such as the zebra mussel and feral pigs, only combined damage and control cost data are available. The damage and control costs are low when compared with the extensive environmental damages these species cause. If we had been able to assign monetary values to species extinctions and losses in biodiversity, ecosystem services, and aesthetics, the costs of destructive nonindigenous species would undoubtedly be several times higher than $137 billion per year. Yet even this understated economic loss indicates that nonindigenous species are exacting a significant toll.

We recognize that nearly all US crop and livestock species are nonindigenous and have proven essential to the viability of the United States' agricultural system and economy. However, the fact that certain nonindigenous crops (e.g., corn and wheat) are vital to agriculture and the US food system does not diminish the enormous negative impacts of other nonindigenous species (e.g., zebra mussel and exotic weeds).

The true challenge for the public lies not in determining the precise costs of the impacts of exotic species but in preventing further damage to natural and managed ecosystems caused by nonindigenous species. Sound prevention policies need to take into account the means through which nonindigenous species gain access to and become established in the United States. Because the modes of invasion vary widely, a variety of preventive strategies will be needed. For example, public education, sanitation, and effective screening and searches at airports, seaports, and other ports of entry will help reduce the chances that biological invaders will become established.

Fortunately, the problem is gaining the attention of policymakers. On 2 February 1999, President Clinton issued an Executive Order allocating $28 million to combat alien species invasions and creating an Interagency Invasive Species Council to produce a plan within 18 months to mobilize the federal government to defend again nonindigenous species invasions. In addition, a Federal Interagency Weed Committee has been formed to help combat nonindigenous plant species invasions (FIWC 1999). The objective of this interagency committee is education, formation of partnerships among concerned groups, and stimulation of research on the biological invader problem. Babbitt (1999) has also established an Invasive Weed Awareness Coalition to combat the invasion and spread of newly introduced non-native plants, such as knapweed (*Centaurea* spp.) and St. John's wort (*Hypericum perforatum*).

Although these policies and practices may help reduce accidental and intentional introduction of potentially harmful exotic species, there is a long way to go before the resources devoted to the problem are in proportion to the risks. We hope that our environmental and economic assessment will advance the argument that investments made now to prevent future introductions will be returned many times over in the preservation of natural ecosystems, diminished losses to agriculture and forestry, and lessened threats to public health.

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