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INTRODUCED SPECIES: A SIGNIFICANT COMPONENT OF HUMAN-CAUSED GLOBAL CHANGE

Summary: Biological invasions are a widespread and significant component of human-caused global environmental change. The extent of invasions of oceanic islands, and their consequences for native biological diversity, have long been recognized. However, invasions of continental regions also are substantial. For example, more than 2,000 species of alien plants are established in the continental United States. These invasions represent a human-caused breakdown of the regional distinctiveness of Earth's flora and fauna - a substantial global change in and of itself. Moreover, there are well-documented examples of invading species that degrade human health and wealth, alter the structure and functioning of otherwise undisturbed ecosystems, and/or threaten native biological diversity. Invasions also interact synergistically with other components of global change, notably land use change. People and institutions working to understand, prevent, and control invasions are carrying out some of the most important - and potentially most effective - work on global environmental change.

Keywords: Biological invasion; Invasions into parks and preserves; Invasion and biological diversity; Invasion and ecosystems; Land-use change; Introduced pests and pathogens.

Introduction

Humans move species beyond their native ranges both deliberately and inadvertently, and many of these species become established and spread in their new habitat. The list of established introduced species grows annually, as does the number of them that cause significant economic and ecological effects. One recent and notorious example in North America is the Eurasian zebra mussel - which like many other aquatic organisms entered in the ballast water of ships, and like many others spread rapidly once it arrived. The invasion of zebra mussels is unusual in the magnitude of its economic consequences; the mussels grow and reproduce rapidly, covering river and lake bottoms and municipal and industrial water inlets. The cost of clearing blocked intake pipes has been calculated to be approximately US\$2 billion (Office of Technology Assessment, 1993). Zebra mussels also alter populations of algae and the concentrations of nutrients in whole ecosystems (Caraco *et al.*, 1997), and they are continuing to spread in rivers, lakes, and canals throughout North America.

We suggest that biological invasions by notorious species like the zebra mussel, and its many less-famous counterparts, have become so widespread as to represent a significant component of global environmental change. This point has been made before (eg Elton, 1958), but is not widely

appreciated, even by the global change research community or by those who study and/or work to control biological invasions. In part, this lack of appreciation reflects the fact that our perception is limited spatially - it is possible to document the presence and importance of biological invasions almost anywhere, but more difficult to perceive that invasions are almost everywhere. In part, it may also reflect a narrow view of global environmental change, one that emphasizes climate change (global warming) at the expense of other, equally significant components of human-caused global change.

In this paper, we place biological invasions in context with other human-caused global environmental changes; briefly describe the global extent of biological invasion; illustrate the consequences of particular invasions as they affect human health and wealth, and/or the functioning and biological diversity of natural ecosystems; discuss interactions between biological invasions and other components of global change; and describe ways that society can prevent, manage, and/or cope with invasions.

Human-caused global environmental change

Our perspective on global environmental change is summarized in Fig. 1, in which the third level lists

six relatively well-documented global changes: the increasing concentration of CO₂ in the atmosphere, alterations to the global biogeochemical cycle of nitrogen and other elements, the production and release of persistent organic compounds such as the chlorofluorocarbons, widespread changes in land use and land cover, hunting and harvesting of natural populations of large predators and consumers, and biological invasions by non-native species. All of these clearly represent ongoing global changes, and all are clearly human-caused.

These changes are driven proximately by the industrial and agricultural enterprises of humanity, and ultimately by the explosive growth over the past two centuries of both the human population and per capita resource use. The six well-documented changes in turn cause other global changes; some drive global climate change by enhancing the greenhouse effect, and some drive loss of biological diversity by causing the extinction of species and genetically distinct populations. The importance of biological invasion as one of these global changes is described here.

The scope and distribution of invasions

How widespread are biological invasions?

The importance of biological invasions to oceanic island ecosystems has long been recognized. Invasions also are frequent in many continental areas, where they represent a substantial component of the flora and fauna of most countries. Table 1 summarizes the pattern and number of plant invasions in many regions. On continents, there is an increase in the number of invading species per log (area) from north to south until one reaches dry subtropical regions; invasions are relatively low in the tropics, then increase again in south temperate areas. Heavily-visited islands are invaded to a greater extent (per log area) than continents or less-trafficked islands. The information in Table 1 confirms patterns illustrated by Rejmánek and Randall (1994). A more general point of Table 1 is that invasions are everywhere, on continents as well

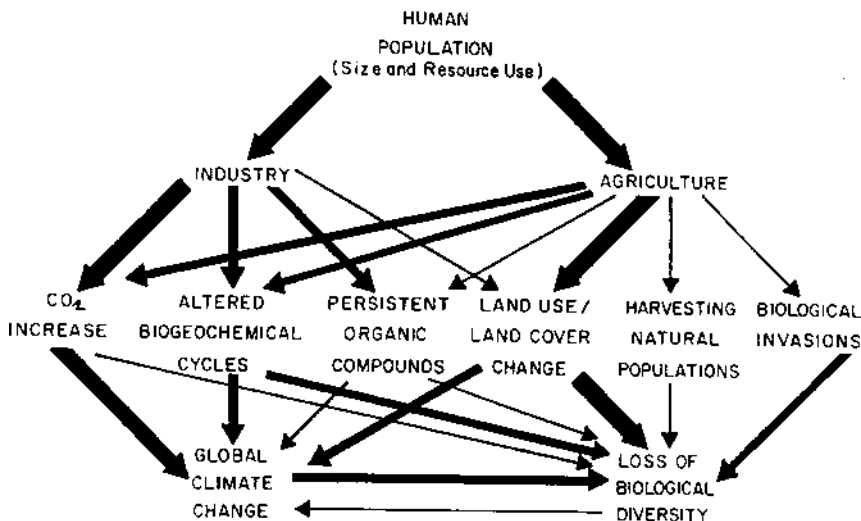


Figure 1: Components of global environmental change. Growth in the size of and resource use by the human population is expressed through growing industrial and agricultural (including forestry, grazing, etc) activity. These have caused a set of relatively well-documented global environmental changes (well-documented both in the sense that they are occurring, and in that they are human-caused), including increasing concentrations of carbon dioxide in the atmosphere, the production and distribution of novel and persistent compounds such as chlorofluorocarbons (with their attendant effects on stratospheric ozone) and PCBs, global-scale alteration of the biogeochemical cycles of nitrogen, sulfur, and other elements, changes in land use and land cover, the removal of top predators from most terrestrial and many marine ecosystems, and biological invasions by exotic species. These components of change interact; they will also drive changes in global climate, and losses of biological diversity. After Vitousek (1994).

Table 1: Established alien vascular plants in selected continental and island floras. Species richness of alien floras is expressed as: (1) The total number of naturalized species. (2) The percentage of naturalized species in the flora. (3) The number of naturalized species/log(area); there is generally an approximately linear relationship between the numbers of species in an area and the log(area). Species that are not established beyond cultivation or which have not been confirmed in this century are not included.

Region/country	Area (km ²)	Number of native species	Number of established alien species	Percentage of established alien species	Number of alien species per log(area)	Sources
LARGE CONTINENTAL AREAS						
Russian Arctic	3,500,000	1,403	104	6.9	15.9	1
Europe	10,382,000	11,820	721	5.7	102.8	2
Western and central Sahara	4,000,000	830	<28	<3.3	<4.2	3
Tropical Africa	22,300,000	23,500	536	2.2	72.9	4
Southern Africa	2,693,389	20,573	824	3.9	128.1	5
Alaska	1,528,200	1,229	144	10.5	23.3	6
Canada	9,976,139	3,270	940	22.3	134.3	7
Coterminous U.S.A.	7,844,400	ca 17,300	ca 2,100	ca 10.8	ca 304.6	8
Peru	1,285,200	17,900	314	1.7	51.4	9
Chile	756,600	4,437	678	13.3	115.3	10
Australia	7,686,848	15,638	1,952	11.1	283.5	11
SMALLER CONTINENTAL AREAS						
Murmansk area	120,000	983	82	7.7	16.1	12
Finland	338,145	1,250	247	16.5	44.7	13
Norway	323,878	1,195	580	32.7	105.3	14
Poland	312,680	2,250	275	10.9	50.1	15
France	549,619	4,350	480	9.9	83.6	16
Egypt	1,000,250	2,015	86	4.1	14.3	17
Djibouti	23,000	641	44	6.4	10.1	18
Uganda	236,040	4,848	152	3.1	28.3	19
Rwanda	26,338	2,500	93	3.6	21.1	20
Namibia	824,293	3,159	60	1.9	10.1	21
Swaziland	17,366	2,715	110	3.9	25.9	22
Cape region	90,000	8,270	441	5.1	88.9	23
NW Territories (Canada)	3,380,000	1,055	53	4.8	8.1	24
British Columbia	948,600	2,048	547	21.1	91.5	25
Ontario	1,068,587	2,056	805	28.1	133.5	26
Minnesota	217,136	1,618	392	19.5	73.5	27
New York	137,795	1,940	1,083	35.8	210.7	28
Missouri	174,242	1,920	634	24.8	121.1	29
California	411,020	4,844	1,025	17.5	182.6	30
Central Florida	68,738	1,746	440	20.1	90.9	31
Texas	692,400	4,498	492	9.9	84.2	32
Baja California	143,700	2,480	183	6.9	35.5	33
Valle de Mexico	7,500	1,910	161	7.8	41.5	34
Chiapas (Mex.)	74,211	6,650	206	3.1	42.3	35
Panama	77,082	7,123	263	3.6	53.8	36
Choco (Colombia)	42,205	3,818	48	1.2	10.4	37
Guaianan	469,234	8,030	287	3.5	50.6	38
Monte Video area	664	843	180	17.6	63.8	39
Buenos Aires area	80,000	1,369	363	21.1	74.1	40
Northern Territory (Australia)	1,331,900	3,293	262	7.4	42.8	41
Queensland	1,707,520	7,535	1,161	13.3	186.3	42
Perth region	10,500	1,510	547	26.6	136.1	43
New South Wales	792,150	4,677	1,253	21.1	212.4	44
Victoria	224,983	2,773	1,190	30.1	222.3	45

Table 1 continued over

Table 1: *continued*

Region/country	Area (km ²)	Number of native species	Number of established alien species	Percentage of established alien species	Number of alien species per log(area)	Sources
ISLANDS						
Devon Is. (Canada)	58,000	115	0	0	0	46
Jan Mayen	380	57	4	6.5	1.6	47
Greenland	326,000	427	86	16.8	15.6	48
Queen Charlotte	9,200	469	116	19.8	29.3	49
British Isles	244,872	1,255	945	42.9	175.4	50
Sakhalin	75,370	1,081	92	7.8	18.9	51
Newfoundland	144,890	906	292	24.4	56.6	52
San Juan Islands (USA)	390	546	283	34.1	109.2	53
Angel Is. (Calif.)	3	282	134	32.2	280.9	54
Santa Cruz (Calif.)	244	462	157	25.4	65.8	55
Crete	8,700	1,586	92	5.5	23.4	56
Canary Islands	7,252	1,254	680	35.2	176.2	57
Bermuda	54	165	303	64.7	174.9	58
Bahamas	14,500	1,104	246	18.2	59.1	59
Hormoz \ Qeshm	1,290	230	49	17.6	15.8	60
Cuba	114,500	5,790	376	6.1	74.3	61
Hawaii	16,764	1,143	891	43.8	210.9	62
Cayman Is.	259	536	65	10.8	26.9	63
Puerto Rico	8,897	2,741	356	11.5	90.1	64
Guadalupe & Martinique	2,620	1,668	360	17.8	105.3	65
Guam	583	327	185	36.1	66.8	66
Ascension	94	25	>120	>82.8	>60.8	67
Galapagos	7,870	604	260	30.1	66.7	68
Rodrigues	40	132	305	69.8	190.4	69
Tristan da Cunha	102	58	119	67.2	59.3	70
Lord Howe	550	206	173	45.6	63.1	71
New Zealand	268,575	2,449	1,623	39.9	298.9	72
Marion \ Prince Edward	330	21	10	32.3	4.1	73
Auckland	450	187	41	17.9	15.5	74
Falklands	11,900	163	83	33.7	20.4	75
Tierra del Fuego	48,700	417	128	23.5	27.3	76
Macquarie Is.	90	44	5	10.2	2.6	77
Southern Shetland Islands	1,390	2	0	0	0	78

Sources: 1. Tolmachev (1960-1987), Gorodkov and Poyarkova (1953-1966); 2. Tutin *et al.* (1964-1980), Tutin *et al.* (1993), Clement and Foster (1994), Rejmánek (unpublished); 3. Ozenda (1991); 4. Lebrun and Stork (1991-1995), Rejmánek (unpublished); 5. Arnold and de Wet (1993); 6. Welsh (1974); 7. Boivin (1968); Scoggin (1978-1979); 8. Kartesz (1994), Morin (1993), Shetler and Skog (1979), U.S. Department of Agriculture (1982); 9. Barko and Zarucchi (1993), Tryon and Stolze (1989-1994); 10. Marticorena and Quezada (1985), Aroyo (unpublished); 11. Hnatiuk (1990); 12. Gorodkov and Poyarkova (1953-1966); 13. Tutin *et al.* (1964-1980), Tutin *et al.* (1993), Ahti and Hämet-Ahti (1971), Suominen (1979); 14. Fremstad, Elven and Tómerås (1994); 15. Kornas (1990); 16. Tutin *et al.* (1964-1980); Tutin *et al.* (1993); Jovet (1971); 17. Täckholm (1974); 18. Lebrun, Audru and Cesar (1989); 19. Rejmánek (unpublished); 20. Troupin (1978-1988); 21. Merxmüller (1966-1972), Roessler and Merxmüller (1976); 22. Kemp (1983); 23. Arnold and de Wet (1993), Bond and Goldblatt (1984); 24. Porsild and Cody (1980); 25. Douglas, Straley and Meidinger (1990-1994); 26. Morton and Venn (1990); 27. Ownbey and Morely (1991); 28. Mitchell (1986); 29. Yatskiewych and Turner (1990); 30. Hickman (1993), Rejmánek and Randall (1994); 31. Wunderlin (1982); 32. Johnson (1990); 33. Wiggins (1980), Gould and Moran (1981); 34. Rzedowski and Rzedowski (1989); 35. Breedlove (1986); 36. D'Arcy (1987); 37. Forero and Gentry (1989); 38. Boggan *et al.* (1992); 39. Lombardo (1982-1984); 40. Cabrera and Zardini (1978); 41. Hnatiuk (1990); 42. Hnatiuk (1990); 43. Marchant *et al.* (1987); 44. Hnatiuk (1990); 45. Carr (1993); 46. Barrett and Teeri (1973); 47. Lid (1964); 48. Porsild (1932), Bøcher *et al.* (1978), Bay (1993); 49. Calder and Taylor (1968); 50. Clement and Foster (1994), Ryves *et al.* (1996); 51. Vorobiev *et al.* (1974); 52. Rouleau and Lamourex (1992); 53. Atkinson and Sharpe (1985); 54. Ripley (1980); 55. Wallace (1985), Junak *et al.* (1995); 56. Barclay (1986); 57. Kunkel (1980); 58. Britton (1918); 59. Correll and Correll (1982); 60. Kunkel (1977); 61. Borhidi (1991); 62. Wagner, Herbst and Sohmer (1990), Wilson (1996); 63. Proctor (1984); 64. Liogier and Martorell (1982), Francis and Liogier (1991); 65. Fournet (1978); 66. Stone (1970), Lee (1974); 67. Duffey (1964), Conk (1980); 68. Lawesson (1990); 69. Strahm (unpublished); 70. Dean *et al.* (1994); 71. Pickard (1984); 72. Atkinson and Cameron (1993); 73. Gremmen (1982); 74. Meurk (1982); 75. Moore (1968); 76. Moore (1983); 77. Selkirk, Seppelt and Selkirk (1990); 78. Komárková, Poncet and Poncet (1990)

as islands, and in the tropics as well as temperate regions. The continental United States and Australia both support ~2,000 species of established alien plants! While the absolute number of species generally is less, introduced plants on some islands make up half or more of the flora.

Biological invasions by fishes and birds are not as frequent as invasions by plants. However, some of the same patterns are evident (Table 2). Isolated islands often support more introduced than native fish species. Even many continental sites (for example, California, Europe and Brazil) have relatively large numbers of non-native fish species. The lack of data on numbers of fish introductions in Africa does not imply that they are unimportant - for example, introduction of Nile perch (*Lates nilotica*) and tilapia (several species in 3 genera) into Lake Victoria has led to dramatic species loss and ecosystem change in a matter of a few decades (Goldschmidt, 1996).

Introduced birds have established wild populations in most countries where data are available, and in some areas (Hawaii, New Zealand) they comprise a substantial proportion of the avifauna. Outside of urban areas, numbers of

introduced bird species are relatively low in most continental regions (compared to islands). However, individual species can be quite abundant in continental habitats - witness the widespread and abundant European house sparrow (*Passer domesticus*) and starling (*Sturnus vulgaris*) in North America.

Invasion Into U.S. Parks and Reserves

Biological invasions are particularly prominent in disturbed areas, leading some to consider invasions to be primarily consequences of disturbance rather than a component of change in their own right. Parks and biological preserves generally represent the least-altered areas of land - a former director of the U.S. National Park Service championed the concept of the parks as a national analogue of "miners' canaries", relatively pristine sites where the pervasiveness of environmental deterioration might be evaluated. What do parks and reserves in the United States tell us about pervasiveness of invasions?

Vascular plants: Floristic lists for a large sample of U.S. reserves have 5 - 25% non-native species. However, the majority of introductions are indeed confined to disturbed areas and appear to

Table 2: *Native and exotic freshwater, inland fish, and breeding bird species in selected regions and countries around the world.*

Region	Area (km ²)	fish ^a			birds ^b		
		native	exotic	reference	native	exotic	reference
Europe	10,400,000		74	1	514	27	11, 12
California	411,020	76	42	2, 3			
Alaska	1,528,200	55	1	4			
Canada	9,976,139	177	9	5			
Mexico	1,958,200	275	26	5			
Australia	7,686,848	145	22	5		32	12
South Africa	3,500,000	107	20	5	900	14	12, 13
Peru	1,285,200		12	6			
Brazil	8,512,000	517	76	7	1,635	2	14
Islands							
Bermuda	54					6	12
Bahamas	14,500				288	4	12, 15
Cuba	114,500		10	6		3	12
Puerto Rico	8,897	3	32	8	105	31	16
Hawaii	16,764	6	19	9	57	38	9
New Zealand	268,575	27	30	10	155	36	17
Japan	372,197		13	6	248	4	12, 18

a Includes only freshwater, inland species.

b Includes only permanent and breeding non-permanent species.

Sources: 1. Holcik (1991); 2. McGinnis (1984); 3. Courtenay *et al.* (1984); 4. Moyle (1986); 5. Macdonald, Kruger and Ferrar (1986); 6. Welcomme, R.L. (1981); 7. Nomura (1984); 8. Erdman (1984); 9. Stone and Stone (1989); 10. McDowall (1984); 11. Jonsson (1993); 12. Long (1981); 13. Roberts (1985); 14. Sick (1993); 15. Paterson (1972); 16. Raffaele (1989); 17. Kinsky (1980); 18. Higuchi, Minton and Katsura (1995).

pose little or no threat to native species or ecosystems (Loope, 1992). In continental areas, the most important exceptions to this generalization include invasions into otherwise little-altered semi-arid areas by grasses, most notably the annual cheatgrass (*Bromus tectorum*), and invasion into riparian habitats and wetlands (i.e. tamarisk in the Southwest, Melaleuca in the Florida Everglades, and purple loosestrife in northeast and midwest) (Loope, 1992). Hawaiian reserves, where the percentage of non-native species in the flora reaches 50 - 70 % and plant invasions clearly threaten native biota, confirm the vulnerability of islands to invasion.

Ungulates: Feral pigs may be the single most damaging introduction in national parks and reserves of the United States. Singer (1981) found that they inhabit 13 areas in the National Park system, in southeastern U.S., Hawaii, and California. Effects of pigs on otherwise undisturbed areas are severe and pervasive in Great Smoky Mountains National Park and in Haleakala and Hawaii Volcanoes National Parks. In Hawaii, pigs are major dispersers and facilitators of plant invaders (Stone, 1985). Other particularly damaging invasive ungulates in parks include feral goats in Hawaii (now largely removed from Hawaiian parks); feral burros in Death Valley (now largely removed), Grand Canyon, and other southwestern parks; and mountain goats (*Oreamnos americanus*) in Olympic National Park.

Aquatic and wetland ecosystems: Invasions of aquatic and wetland ecosystems of continental U.S. are fully as severe as island invasions. In Sequoia-Kings Canyon National Park, for example, intentionally introduced brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) have displaced native rainbow trout (*Onchorhynchus mykiss*) in many streams (G. Larson, personal communication). Brook and rainbow trout introduced in waters previously barren of fish have greatly reduced native invertebrate organisms and amphibians. In Great Smoky Mountains National Park, the introduced rainbow trout threatens native brook trout populations with local extirpation (G. Larson, personal communication). Even the relatively pristine waters of Glacier National Park have been largely (84 %) compromised by past fish introductions (Marnell, 1995).

Forest pathogens and insects: White pine blister rust (*Cronartium ribicola*) and the balsam woolly adelgid (*Adelges piceae*) illustrate the devastating effects of introduced forest "pests", even in undisturbed parks and preserves. Both were brought to the U.S. 80—100 years ago on European nursery stock, and (after years of harm to commercial forest concerns) both are now affecting U.S. parks and reserves.

White pine blister rust attacks five-needled pines; it is now causing increasing mortality of sugar pine (*Pinus lambertiana*) in forests of Yosemite and Sequoia-Kings Canyon National Parks (L. Bancroft, pers. comm.). Whitebark pine (*P. albicaulis*) also is being hit hard; fewer than one tree in 10,000 is rust resistant, and large die-offs are expected to occur through the range of whitebark pine. Since whitebark pine seeds are an extremely important food of the grizzly bear and other animals (Kendall, 1995), decline of the tree may have severe consequences in Glacier, Yellowstone and Grand Teton National Parks.

Balsam woolly adelgid attacks true firs of the genus *Abies*, causing mortality within 2—7 years through feeding and chemical damage to vascular tissue. This small cottony insect is particularly damaging to Fraser fir (*Abies fraseri*), a species found only in the southern Appalachian Mountains, where it occurs primarily within the high-elevation spruce-fir forest of Great Smoky Mountains National Park. Since its discovery in 1963 in the park, the adelgid has killed nearly all adult (cone-bearing) fir trees in the park (Langdon and Johnson, 1992).

Consequences of invasions

The number and variety of species introductions makes clear that it is no exaggeration to say biological invasions are breaking down the biogeographic barriers that have created and maintained the major floral and faunal regions of Earth. In other words, invasions are blurring the regional distinctiveness of Earth's biota. However, while all human-caused biological invasions represent environmental change, we are not equally concerned about the consequences of all of them. Many invasions are reflections of other changes, rather than being themselves drivers of change. For example, invading plants that only occupy roadside areas cannot now be regarded as serious threats to native biological diversity; they are a consequence of land-use change (which may itself threaten diversity). Moreover, some introduced species clearly are beneficial to humanity; for example, it would be impossible to support the present population of the United States entirely on native foods. However, some invading species degrade human health and/or wealth directly; others affect the structure and functioning of ecosystems, and/or the maintenance or restoration of native biological diversity. We will discuss an example of each of these, to illustrate some of the consequences of current invasions. For each that we discuss, there are many others that are at least as well documented and at least as damaging.

Human Health

Most infectious diseases themselves are human-transported biological invaders over most of their range. Several centuries ago, the indigenous people of North America could have cited smallpox as a devastating Old World invader (Crosby, 1986) - just as modern Americans can point to HIV.

Introduced species themselves can act as vectors of disease. One recent example is the Asian tiger mosquito *Aedes albopictus*. Its larvae were brought into the United States as hitch-hikers in used car and truck tires imported for retreading and resale (Craven *et al.*, 1988). Two earlier introductions of *A. albopictus* in shipments of military tires had failed to establish - but with the growth of commercial importation, *A. albopictus* and other mosquitoes have been imported more frequently (6.8 tires/10,000 were found to be infested in 1986), and over a much wider area (Craven *et al.*, 1988). *A. albopictus* became established in the U.S. in the 1980s, and as of 1992 occurred in 25 states. It can feed on most mammals and birds; in its natural range, it is a known vector of dengue fever and other human arboviruses. Perhaps most importantly, in the U.S. it is a documented vector for eastern equine encephalitis, an often-fatal viral infection of people as well as horses (Craig, 1993).

Wealth

The zebra mussel invasion mentioned above is a recent invasion that has been expensive for North American cities and industries. Other invasions affect crops, rangelands, and commercial forests, costing many millions of dollars annually in lost yields and control efforts. Invasions can also be costly to developing economies, where the margin for dealing with additional costs is less. One example is the golden snail (*Pomacea canaliculata*) in Asian rice ecosystems. The snail was brought from South America to Taiwan to provide a supplemental source of protein and export income to small rice farms. Its benefits were illusory - local people find the snail distasteful (a recipe calling for "washing in a vinegar solution repeatedly to remove mucus and slime" may help to explain why), and the export market was closed by health concerns (Food and Agricultural Organization, 1989). At the same time, the costs of golden apple snail importation were high - the snail has rapid population growth, spreads rapidly through irrigation canals, and voraciously consumes young rice plants. When the costs became clear, the entrepreneurs who imported the snail simply exported it to other countries; it has now spread throughout east and southeast Asia (Fig. 2).

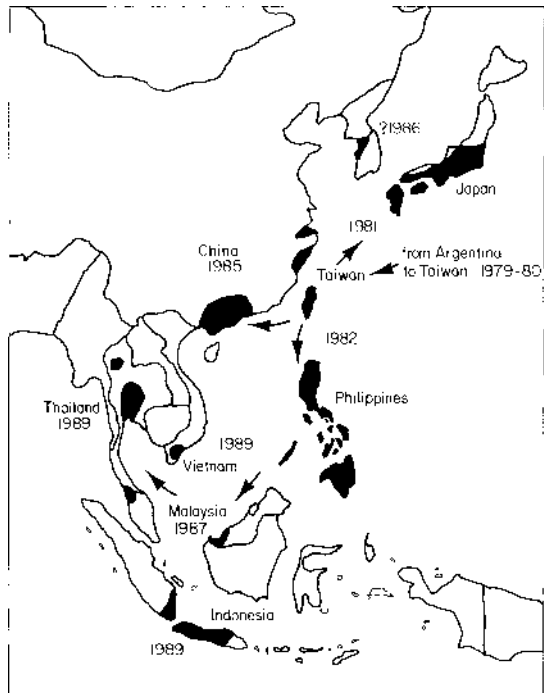


Figure 2: Distribution and spread of the golden apple snail through Asian rice-growing countries. From Naylor (1996).

The economic costs of this invasion have been evaluated carefully in the Philippines (Naylor, 1996). In 1990 alone, the total cost to farmers was \$27.8–45.3 million, split among costs of control with molluscicides and handpicking, replanting costs, and yield losses (despite control and replanting). This amounted to 25–40 % of what the Philippines spent on rice imports in 1990; it represents just one year's damage in one of many infested countries.

Ecosystem effects

Invaders that alter ecosystem processes such as primary productivity, decomposition, hydrology, geomorphology, nutrient cycling and/or disturbance regimes do not simply compete with or consume native species - they change the rules of existence for all species. Invaders that affect each of these processes are known; we cannot discuss all of them here, but one dramatic example is the invasion of the nitrogen-fixing tree *Myrica faya* into Hawaii Volcanoes National Park. Seeds of *Myrica* are dispersed by a variety of native and introduced birds,

and thereby readily reach young sites created by volcanic eruptions. Studies in Hawaii Volcanoes National Park show that: 1) plant growth in young volcanic sites is profoundly limited by low N availability in soil; 2) colonization by *Myrica* increases total inputs of N by more than 4-fold; 3) the N fixed by *Myrica* cycles rapidly through *Myrica* and to biologically available pools in the soil (Vitousek and Walker, 1989); and 4) the N that *Myrica* adds to sites alters community composition of other plant species, and of soil organisms - in both cases towards dominance by other non-native organisms. In essence, invasion by one species changes the composition and dynamics of the entire ecosystem (Vitousek and Walker, 1989).

Effects on Biological Diversity

The eastern deciduous forests of North America represent a diverse continental ecosystem, one that might be expected to be as resistant as any to biological invasions. These forests were cleared extensively in the 1800s, but have recovered substantially in this century. The scientific community has put a great deal of effort into determining current and probable future effects of climate change, increased CO₂ concentrations, acid rain, and oxidant air pollution on these forests. However, by far the greatest perturbations to these ecosystems in this century have involved the invasion of wave after wave of introduced pests and diseases (Sinclair, Lyon and Johnson, 1987, Campbell and Schlarbaum, 1994, Niemelä and Mattson 1996). Some of these pests, such as gypsy moth (*Lymantria dispar*), consume a variety of species, and their effects on forest diversity are not yet known. Other more specialized pathogens have eliminated the American chestnut, *Castanea dentata* (once a dominant component of eastern forests) and American elm, *Ulmus americana* from the eastern forest. Other tree species undergoing major decline due to non-native diseases or insects include American beech (*Fagus grandifolia*), mountain ash (*Sorbus americana*), butternut (*Juglans nigra*), eastern hemlock (*Tsuga canadensis*), flowering dogwood (*Cornus florida*), and sugar maple (*Acer saccharum*) (Langdon and Johnson, 1992, Campbell and Schlarbaum, 1994) - in addition to the Fraser fir discussed above. We suspect that invasions will continue to represent the most important factor reducing diversity of these forests for the foreseeable future.

Interactions With Other Global Changes

In addition to being a component of global change, biological invasions interact with the other major

components of change (Huenneke, 1996). We discuss interactions with two of these - land use change and extinction/loss of biological diversity.

Land Use Change

Biological invasions interact with land-use change in several ways. The most obvious of these is through human alteration of disturbance regimes. The association between disturbance and invasion was noted above - and humans are now the premier agents of disturbance on the planet. Moreover, we have not merely increased the frequency and/or intensity of disturbance; in many cases we have created types of disturbances that are unlike anything in the evolutionary history of many species. These alterations have promoted invasion, often by species that are associated with similar disturbances within their original range (Hobbs and Huenneke, 1992).

The interaction between land use change and invasion is not a one-way street. Both introduced plants and animals can alter the disturbance regime of sites they invade (D'Antonio *et al.*, in press). For example, introduced fire-promoting grasses have invaded many arid or semi-arid ecosystems, and in so doing have increased the frequency, size and/or intensity of fires. A recent literature review concluded that non-native, fire-promoting grasses are common in the Americas, Australia and Oceania, where they threaten the maintenance of remaining seasonally-dry tropical forests in some areas, and represent a major impediment to the restoration (even reforestation) of cleared lands (D'Antonio and Vitousek, 1992). The dynamics of the introduced grass/fire cycle are summarized in Fig. 3. In this scenario, initial disturbance such as land clearing (which often utilizes fire) allows the invasion of introduced grasses. These grasses then create microclimate and fuel conditions that favor an increased frequency of fire. Fire in turn selects against many native species and further promotes fire-adapted grasses, resulting in a positive feedback that perpetuates low diversity grassland or savanna.

External disturbance is not always required to set this feedback in motion - at least in some cases, grass invasion in and of itself is sufficient to enhance fuel loading and increase the probability of fire. It is even possible for grass species to promote human-caused land use change. For example, the ready availability of forage grasses that withstand grazing and drought conditions has led to the conversion of millions of hectares of Sonoran desert woodland to near monocultures of African buffel grass (*Cenchrus ciliaris*, also called *Pennisetum ciliare*). (Yetman and Burquez, 1994). Likewise, in Central and South America dry and mesic forests have been replaced

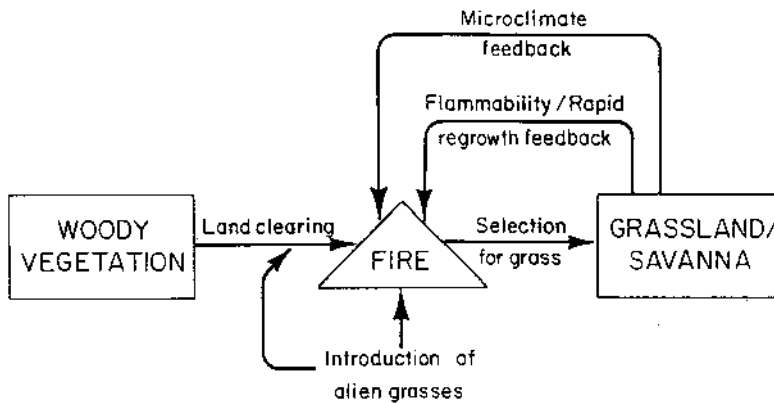


Figure 3: Land clearing and grass invasions can interact in the initiation and maintenance of a grass-fire feedback system that prevents forest regeneration over large areas of Earth. From D'Antonio and Vitousek (1992).

by grazing tolerant (and fire responsive) African pasture grasses (Parsons, 1972).

Perhaps the most dramatic and well documented example of an introduced grass/fire cycle is the invasion of the intermountain west in North America by the European cheatgrass (*Bromus tectorum*). This annual species invaded shrub/steppe habitat in the Great Basin that was previously dominated by native shrubs and native perennial grasses. After cheatgrass invasion, fire frequency has increased from an estimated once every 60–110 yr to once every 3–5 yr. Almost 5 million hectares of land in Idaho and Utah are now nearly monospecific stands of cheatgrass (Whisenant, 1990).

The suppression of disturbance can also promote invasion by introduced species, particularly in aquatic ecosystems where reproduction and recruitment are often synchronized with disturbance cycles. Indeed, the damming and impoundment of most of the rivers in the U.S. has been correlated with the invasion of rivers, streambanks and floodplains by introduced species, and with the rapid conversion of diverse, native riparian forests to low diversity stands of introduced species. For example, prior to the construction of the large network of dams that control the Colorado river, its floodplain forests were dominated by native cottonwood and willow species. With dam construction, groundwater tables have dropped, scouring floods have ceased and cottonwood and willow have declined - and been replaced by nearly monospecific stands of the introduced saltcedar (*Tamarix* sp.) (Ohmart, Anderson and Hunter, 1988).

The fragmentation of wildland habitat resulting from agricultural or urban development has also

affected the spread of introduced species. Urban forests and parklands represent an increasing percentage of our remaining near-natural habitats. Because they are subjected to pollution stresses and because of their proximity to sites of introduction and their (often) large ratio of edge to interior habitat, they are prime habitat for introduced plant or animal pests which can then spread into less urban habitat. Gypsy moths, for example, first became established in an urban forest and subsequently became a major pest species throughout the eastern United States (see Liebhold *et al.*, 1995 for a history of the gypsy moth outbreak). Outbreaks of introduced fungal pathogens have also been found to be more common in forest fragments that are close to urban areas (Castello, Leopold and Smallidge, 1995).

Invasion and Extinction

A greatly enhanced rate of extinction of species and of genetically distinct populations is the least reversible of the many ongoing global environmental changes (Vitousek, 1994) - and there is good evidence that biological invasions contribute substantially to extinction. As of 1991, 44 species of freshwater fish in the continental United States were threatened or endangered by the introduction of non-native fish. Of the 40 species of fish known to have gone extinct since 1890, 27 were negatively affected by introduced fish (Wilcove and Bean, 1994).

While most extinctions in which introduced species are known to have played a major part have been on islands or in aquatic systems, the potential for invasion-driven extinctions in continental systems is substantial. At a global scale, this impact can be estimated using species - area curves. These

summarize the relationship between the size of an area (an island or isolated patch of habitat) and the number of species it supports. Preston (1960) plotted the number of species of breeding birds in different habitats against log of the area supporting them, and found a linear relationship. Extrapolating that relationship to the area of Earth's land surface yields a total number of bird species that is substantially less than the actual number. The difference comes about because areas that are isolated from each other support wholly different bird faunas - in other words, because regional distinctiveness begets global diversity.

Westbrooks and colleagues applied this approach to calculate directly the potential for extinction resulting from biological invasion; Wright (1987) had earlier carried out a similar analysis. For example, a plot of the number of mammalian species on each continent versus log area yields a straight line with $r^2 = .94$; extending this relationship to the land area of Earth, a single supercontinent would support ~2,000 species (Fig. 4). Earth's continents in fact support 4,200 species, due to isolation of distinct faunas in different regions. This analysis implies that if invasions were so widespread as to cause a complete breakdown of the biogeographic barriers separating different regions, a substantial number of Earth's mammalian species would (ultimately) be driven to extinction.

We believe that this analysis is as solid as estimates of potential extinction rates based on habitat loss and fragmentation (Wilson, 1992). Moreover, this approach is supported by paleobiological evidence. Two or three million years ago, the Isthmus of Panama connected North and South America, and allowed a massive exchange of their biota (at least, of that portion able to survive in the tropics) (Simpson, 1980). The result was asymmetrical - while some South American mammals (notably the opossum) spread and thrived in North America, many more North American mammals spread through South America. This invasion by North American mammals corresponded with a significant increase in the extinction rate of South American mammals (Marshall *et al.*, 1982).

What Can Be Done?

In discussing biological invasions with other scientists and the public, we run into two major concerns. The first is a belief that invasions represent a natural process that has always been with us; the second is the feeling that the ease of travel and the increasing global nature of the economy make it impossible to prevent invasions for long.

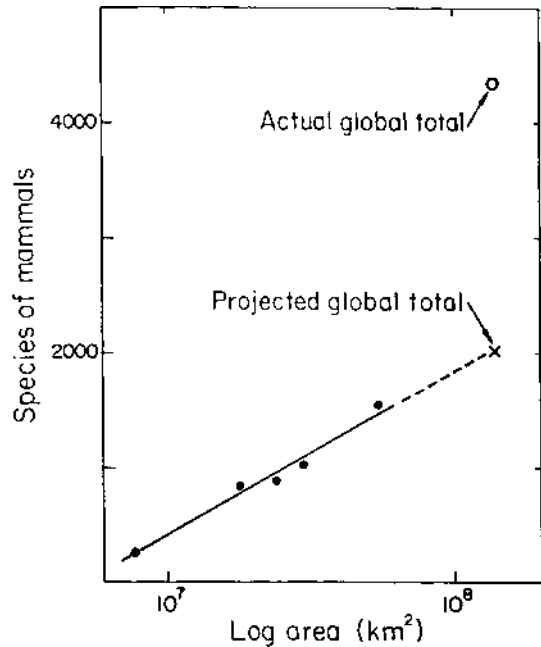


Figure 4: A species/area curve for mammals. The number of species on a continent is tightly correlated with the size of that continent - but extrapolating that relationship to the land area of Earth (reuniting Gondwanaland) yields less than half the total number of species that actually occur on these continents. Much of the diversity of mammalian species globally is due to the isolation of separate biotic regions. Analysis prepared by A. Laurer of the Center for Conservation Biology, Stanford University.

For the first, it is of course true that invasions (like extinctions) have always been with us. What differs now is the increased rate of invasions, resulting from the extraordinary mobility of humanity and our goods - an increase in the rate of invasions that is so large as to represent a difference in kind rather than degree. For example, the complete insect fauna of the Hawaiian Islands resulted from a successful colonization (followed by evolutionary radiation) every 50,000–100,000 years - but recently, 15–20 insect species per year have become established there (Beardsley, 1979). Similarly, detailed paleoecological studies of Eastern North America indicate that there was one prehistoric instance (in the past 10,000 years) in which a tree species (eastern hemlock) declined precipitously in a pattern consistent with pathogen attack throughout most of its range (Davis, 1981). This contrasts with devastation of several American tree species by pathogens in the past century.

For the second concern, we have framed the problem of biological invasions as a fundamental component of human-caused global change, important in driving global losses of biological diversity as well as (in many cases) undesirable from a purely anthropocentric viewpoint (health, wealth). As with other types of human-caused global change, stemming the tide of biological invasions poses a huge challenge to the ingenuity of humankind. A large part of the task is convincing our colleagues, students, and the public that it is a problem worthy of our best efforts, and giving them sufficient understanding that they can respond in a positive way. Government-directed efforts are not going to work without widespread support from citizens. Our experience suggests that such citizen support in beginning to arise in the United States, in the areas that have been hardest hit by invasions. In Hawaii and Florida, invasion stories are front-page items in local newspapers, County Councils have been known to provide funds for emergency invasive species control projects to assure protection of biodiversity, local lifestyles, and tourism.

Several of us attended an international conference on alien species in Norway in mid-1996 and were encouraged by the high level of concern accorded the problem in many countries and by a number of serious efforts being initiated to confront it at international, national, and local levels. (See Sandlund, Schei and Viken 1996.) Better legal frameworks are being sought in several countries. New Zealand's Biosecurity Act of 1993 and Hazardous Substances and New Organisms Act of 1996 are recognized as outstanding examples of progressive legislation.

The challenge of slowing invasions may prove to be as rewarding as - but less threatening to economic growth and lifestyles than - slowing fossil fuel combustion. Existing national laws and policies can be enforced and strengthened, and intelligent new approaches can be devised, given reasonable public support. Moreover, concerned and informed citizens can participate personally in recognizing incipient invaders and preventing them from spreading. The concept of thinking globally but acting locally applies extremely well to stopping invasions. Perhaps with no other form of global change can educated and dedicated individuals have such an opportunity to make a lasting difference.

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