

Issues in Ecology

TECHNICAL REPORT

BIOTIC INVASIONS: CAUSES, EPIDEMIOLOGY, GLOBAL CONSEQUENCES, AND CONTROL

RICHARD N. MACK,¹ DANIEL SIMBERLOFF,² W. MARK LONSDALE,³ HARRY EVANS,⁴ MICHAEL CLOUT,⁵ AND FAKHRI A. BAZZAZ⁶

¹*School of Biological Sciences, Washington State University, Pullman, Washington 99164 USA*

²*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996-1610 USA*

³*CSIRO Entomology and CRC for Weed Management Systems, GPO Box 1700, Canberra, ACT 2601, Australia*

⁴*CABI BIOSCIENCE, UK Centre (Ascot), Silwood Park, Buckhurst Road, Ascot, Berkshire SL5 7TA, UK*

⁵*School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand*

⁶*Biological Laboratories, Harvard University, 16 Divinity Avenue, Cambridge, Massachusetts 02138 USA*

Abstract. Biotic invaders are species that establish a new range in which they proliferate, spread, and persist to the detriment of the environment. They are the most important ecological outcomes from the unprecedented alterations in the distribution of the earth's biota brought about largely through human transport and commerce. In a world without borders, few if any areas remain sheltered from these immigrations.

The fate of immigrants is decidedly mixed. Few survive the hazards of chronic and stochastic forces, and only a small fraction become naturalized. In turn, some naturalized species do become invasive. There are several potential reasons why some immigrant species prosper: some escape from the constraints of their native predators or parasites; others are aided by human-caused disturbance that disrupts native communities. Ironically, many biotic invasions are apparently facilitated by cultivation and husbandry, unintentional actions that foster immigrant populations until they are self-perpetuating and uncontrollable. Whatever the cause, biotic invaders can in many cases inflict enormous environmental damage: (1) Animal invaders can cause extinctions of vulnerable native species through predation, grazing, competition, and habitat alteration. (2) Plant invaders can completely alter the fire regime, nutrient cycling, hydrology, and energy budgets in a native ecosystem and can greatly diminish the abundance or survival of native species. (3) In agriculture, the principal pests of temperate crops are nonindigenous, and the combined expenses of pest control and crop losses constitute an onerous "tax" on food, fiber, and forage production. (4) The global cost of virulent plant and animal diseases caused by parasites transported to new ranges and presented with susceptible new hosts is currently incalculable.

Identifying future invaders and taking effective steps to prevent their dispersal and establishment constitutes an enormous challenge to both conservation and international commerce. Detection and management when exclusion fails have proved daunting for varied reasons: (1) Efforts to identify general attributes of future invaders have often been inconclusive. (2) Predicting susceptible locales for future invasions seems even more problematic, given the enormous differences in the rates of arrival among potential invaders. (3) Eradication of an established invader is rare, and control efforts vary enormously in their efficacy. Successful control, however, depends more on commitment and continuing diligence than on the efficacy of specific tools themselves. (4) Control of biotic invasions is most effective when it employs a long-term, ecosystem-wide strategy rather than a tactical approach focused on battling individual invaders. (5) Prevention of invasions is much less costly than post-entry control. Revamping national and international quarantine laws by adopting a "guilty until proven innocent" approach would be a productive first step.

Failure to address the issue of biotic invasions could effectively result in severe global consequences, including wholesale loss of agricultural, forestry, and fishery resources in some regions, disruption of the ecological processes that supply natural services on which human enterprise depends, and the creation of homogeneous, impoverished ecosystems composed of cosmopolitan species. Given their current scale, biotic invasions have taken their place alongside human-driven atmospheric and oceanic alterations as major agents of global change. Left unchecked, they will influence these other forces in profound but still unpredictable ways.

Key words: *alien species; biological control; biotic invaders; eradication; global change; immigration; invasion; naturalization; nonindigenous; pests; weeds.*

Manuscript received 4 November 1999; accepted 4 November 1999.

Reprints of this 22-page report are available for \$3.25 each. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1707 H Street, N.W., Suite 400, Washington, DC 20006.

INTRODUCTION

Biotic invasions can occur when organisms are transported to new, often distant, ranges where their descendants proliferate, spread, and persist (*sensu* Elton 1958). In a strict sense, invasions are neither novel nor exclusively human-driven phenomena. But the geographic scope, frequency, and the number of species involved have grown enormously as a direct consequence of expanding transport and commerce (Wells et al. 1986, di Castri 1989). Few habitats on earth remain free of species introduced by humans (e.g., Surtsey [Fridriksson and Magnusson 1992]); far fewer are so remote or display such unique environments that they can be considered immune from this dispersal (e.g., locales above 80° latitude). The number of species that have entered new ranges through human agency has increased by orders of magnitude in the past 500 years, and especially in the past 200 years (di Castri 1989), thanks to expanding human migrations and commerce. Nonindigenous species represent an array of taxonomic categories and geographic origins that defy any ready classification (Crawley 1987, Long 1981, Holm et al. 1997).

The adverse consequences of biotic invasions vary enormously. At one extreme, the mere presence of nonindigenous species in a conservation reserve could be deemed detrimental. Invaders can alter fundamental ecological properties such as the dominant species in a community and an ecosystem's physical features, nutrient cycling, and plant productivity (Bertness 1984, Vitousek 1990). The aggregate effects of human-caused invasions threaten efforts to conserve biodiversity (Walker and Steffen 1997), maintain productive agricultural systems (U.S. Congress 1993), sustain functioning natural ecosystems (D'Antonio and Vitousek 1992, Vitousek et al. 1996), and also protect human health (Soulé 1992). However, as a practical rather than conceptual restriction, we do not deal here with the invasive parasites of humans. We outline below the epidemiology of invasions, hypotheses on the causes of invasions, the environmental and economic toll they take, and tools and strategies for reducing this toll.

THE EPIDEMIOLOGY OF INVASIONS

Biotic invasions constitute only one outcome—indeed, the least likely outcome—of a multistage process that begins when organisms are transported from their native ranges to new locales. These immigrant organisms and their descendants have been referred to as “alien,” “adventive,” “exotic,” “neophytes” (in the case of plants), “introduced,” and most recently, “nonindigenous” (Salisbury 1961, Mack 1985, Baker 1986, U.S. Congress 1993). These terms have been used interchangeably and often without careful distinction. We will employ “nonindigenous” as the most general term for immigrant species, especially where their invasive status is uncertain.

The fates of these organisms vary vastly. First, many, if not most, perish en route to a new locale (e.g., propagules suspended in marine ballast water). If they succeed in reaching a new site, immigrants are likely to be destroyed quickly by a multitude of physical or biotic agents (Kruger et al. 1986, Mack 1995). It is almost impossible to obtain data quantifying the number of species that are actually dispersed from their native ranges, the number of emigrants that subsequently perish, and the number of arrivals. But based on the number of species that have been collected only once far beyond their native range (e.g., Thellung 1911–1912, Ridley 1930, Carlton and Geller 1993), the local extinction of immigrants soon after their arrival must be enormous.

Despite such wholesale destruction either in transit or soon after arrival, immigrants occasionally survive to reproduce. Even then, their descendants may survive for only a few generations before going extinct locally. Again, however, some small fraction of these immigrant species do persist and become naturalized. At that point, their persistence does not depend on recurring, frequent re-immigration from the native range (Lousley 1953). These populations' minimum size, number, and areal extent have no commonly identified thresholds, although a greater number and frequency of new arrivals do raise the probability that a species will establish permanently (Veltman et al. 1996). Among the naturalized species that persist after this extremely severe reductive process, a few will go on to become invaders.

A comparison is often made between epidemics caused by parasites and all other biotic invasions because many important factors in disease epidemiology are common to all invasions. These factors include identity of the vectors, the parasite's minimum viable population size, the time course and character of its population growth and spread, the fate of interacting species in the new range (including their coevolution), and mitigating (or exacerbating) effects of the new environment. All have direct parallels in studying invasions, regardless of the species (Mack 1985). Below we explore the epidemiology and the underlying mechanisms that allow some species to become invaders.

Humans as dispersal agents of potential invaders

Humans have served as both accidental and deliberate dispersal agents for millennia, and the dramatic increase in plant, animal, and microbial immigrations worldwide roughly tracks the rise in human transport and commerce (di Castri 1989, U.S. Congress 1993). Ancient human migrations and trade led to the early spread of some domesticated species such as cereals, dates, rice, cattle, and fowl, along with the inadvertent spread of their parasites (diCastri 1989, Zohary and Hopf 1993). Beginning around 1500, Europeans transported Old World species to their new settlements in

the Western Hemisphere and elsewhere. The manifests from Columbus' second and subsequent voyages, for instance, indicate deliberate transport of species regarded as potential crops and livestock (Crosby 1972). Global commerce has grown meteorically since the late 15th century, as indexed by the rise in shipping tonnage (Fayle 1933); this growth has provided an opportunity for a corresponding growth in biotic invasions. Given the magnitude of this transport and subsequent naturalizations of species in new lands, biotic invasions can be viewed as predominantly post-Columbian events.

The human-driven movement of organisms over the past 200 to 500 years, deliberate and accidental, undoubtedly dwarfs in scope, frequency, and impact the movement of organisms by natural forces in any 500-year period in the earth's history. Such massive alteration in species' ranges rivals the changes wrought by continental glaciation and deglaciation cycles of past ice ages, despite the fact that these human-driven range shifts have occurred over much less time (e.g., Semken 1983).

The proportion of various types of organisms that have invaded as a result of accidental vs. deliberate movement clearly varies among taxonomic groups (Moyle 1986, Heywood 1989). Few, if any, invasive microorganisms have been deliberately introduced. Deliberate microbial introductions have instead most commonly involved yeasts for fermentation or mutualists, such as mycorrhizal fungi (Read et al. 1992). Among insects, some deliberate introductions have had adverse consequences, including bumble bees in New Zealand (Thompson 1922), but the majority of invasive insects have probably been accidentally introduced. Introductions of marine invertebrates probably mirror insects. A few deliberate introductions have been made (e.g., the Pacific oyster [*Crassostrea gigas*] imported from Japan to Washington State), but a growing number of invaders such as the zebra mussel (*Dreissena polymorpha*) have arrived as accidental contaminants in ship ballast (Carlton and Geller 1993). In contrast, most invasive vertebrates, principally fish, mammals, and birds, have been deliberately introduced. Some of the worst vertebrate invaders, however, have been spread accidentally: *Rattus rattus*, *Rattus norvegicus*, the brown tree snake (*Boiga irregularis*), the sea lamprey (*Petromyzon marinus*) (Brown 1989). Some invasive plants have been accidentally introduced as contaminants among crop seeds and other cargo (e.g., *Parthenium hysterophorus*, *Rottboellia cochinchinensis*) (Huelma et al. 1996). However, many, if not most, plant invaders in the United States have been deliberately introduced, including some of the worst pests: *Eichhornia crassipes*, *Sorghum halapense*, *Melaleuca quinquevneria*, and *Tamarix* spp. (R. N. Mack, unpublished data).

The prominence of deliberately introduced species that later become biotic invaders emphasizes that not

all pests arrive unheralded and inconspicuously; many are the product of deliberate but disastrously flawed human forethought (Fig. 1).

The transformation from immigrant to invader

The progression from immigrant to invader often involves a delay or lag phase, followed by a phase of rapid exponential increase that continues until the species reaches the bounds of its new range and its population growth rate slackens (Mack 1985, Cousens and Mortimer 1995; Fig. 2). This simplified scenario has many variants. First, some invasions such as those by Africanized bees in the Americas and zebra mussels in the Great Lakes may go through only a brief lag phase, or none at all (Crooks and Soule 1996). On the other hand, many immigrant species do not become abundant and widespread for decades, during which time they may remain inconspicuous. Perhaps the most spectacular example involves the fungus, *Entomophaga maimita*, introduced to the United States for control of the gypsy moth (*Lymantria dispar*). After effectively disappearing for 79 years, it made a reappearance in 1989 and is now inflicting substantial mortality on the moth in the northeastern United States (Hajek et al. 1995). Brazilian pepper (*Schinus terebinthifolius*) was introduced to Florida in the 19th century but did not become widely noticeable until the early 1960s. It is now established on >280 000 ha in south Florida, often in dense stands that exclude all other vegetation (Schmitz et al. 1997).

During the lag phase, it can be difficult to distinguish doomed populations from future invaders (Cousens and Mortimer 1995). Most extinctions of immigrant populations occur during the lag phase, yet the dynamics of such a population are often statistically indistinguishable from those of a future invader, which is growing slowly but inexorably larger. This similarity in the size and range of these populations frustrates attempts to predict future invaders while they are few in numbers and presumably controllable.

Whether most invasions endure lag phases, and why they occur, remain conjectural (Williamson 1996). Any lag phase in the population growth and range expansion for a potential invasion most likely results from several forces and factors operating singly or in combination:

1) *Limits on the detection of a population's growth.* A lag could be perceived simply through the inability to detect still small and isolated but nonetheless growing populations in a new range (Crooks and Soule 1996).

2) *The number and arrangement of infestations of immigrants.* Usually an invasion will proceed fastest from among many small, widely separated infestations or foci compared with a single larger one (Moody and Mack 1988). Unless many foci arise soon after immigration, an unlikely event, the lag phase could be

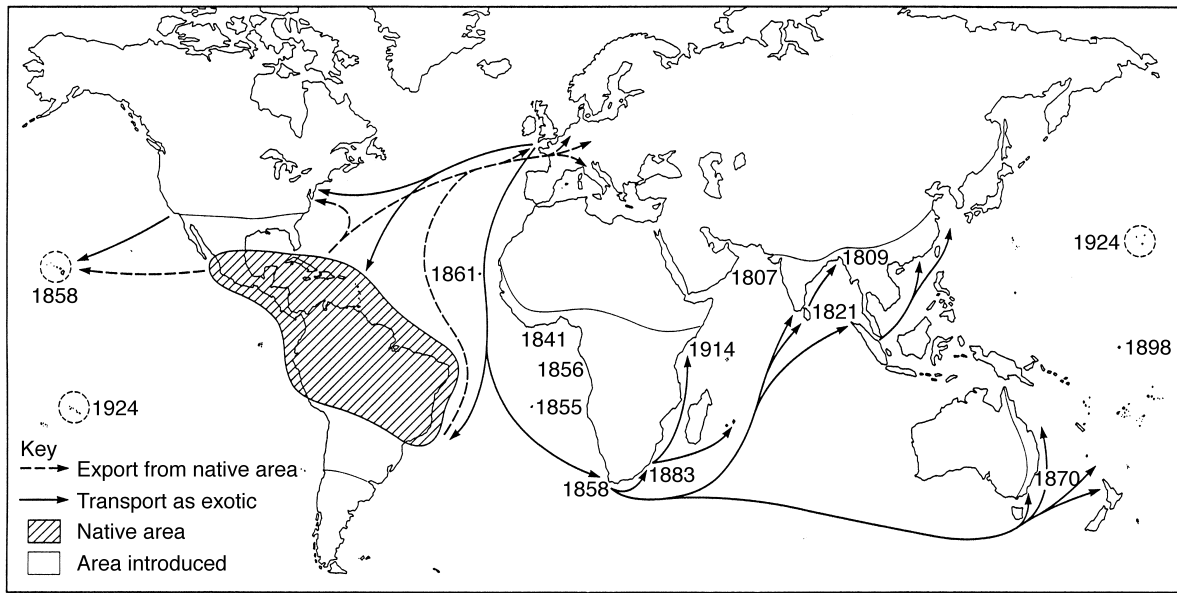


FIG. 1. Some invaders have widely separated new ranges, the products of repeated human dispersal and cultivation. For example, the shrub *Lantana camara* was carried transoceanically throughout the 19th and early 20th century to many subtropical and tropical locales where it has proliferated. Years refer to dates of introduction in widely separated locales (Cronk and Fuller 1995).

the result of an initial limitation in widely separated foci.

3) *Natural selection among rare or newly created genotypes adapted to the new range.* Strong selection in a new range may simply destroy all but the few pre-adapted genotypes, thus accounting in part for the very high extinction rate among immigrant populations. Alternatively, the lag phase could reflect the time for emergence of new genotypes through outcrossing among immigrants, although proof of this explanation has proven elusive (Baker 1974, Crooks and Soule 1996).

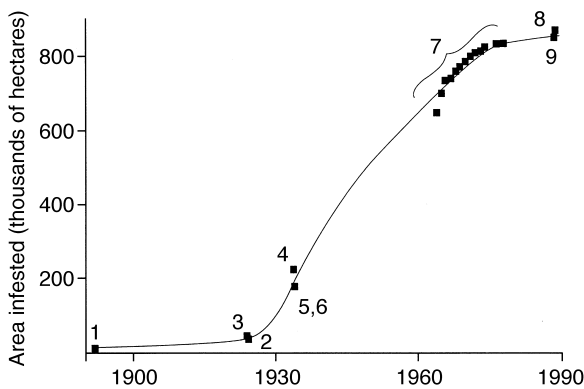


FIG. 2. Many invaders occupy new ranges at an accelerating rate with pronounced "lag" and "log" phases of proliferation and spread. Terrestrial plant invasions most commonly illustrate this pattern (e.g., the spread of *Opuntia aurantiaca* in South Africa [Moran and Zimmerman 1991]).

4) *The vagaries of environmental forces.* The order, timing, and intensity of environmental hazards are critical for all populations, but the consequences of consecutive periods of high mortality are most severe among small populations. Thus, a small immigrant population could persist or perish largely as a consequence of a lottery-like array of forces across time and generations: i.e., whether the first years in the new range are benign or severe; whether environmental forces combine to destroy breeding-age individuals as well as their offspring. Immigrant populations may also be so small that demographic stochasticity, simply the odds that few, if any, reproductive individuals will produce offspring as influenced by endogenous forces, can also be important (Simberloff 1988). Much of the downward spiral seen in the size of immigrant populations could be attributed simply to the single and collective action of these two forces (Mack 1995).

Clearly, some populations overcome these long odds and grow to a threshold size such that extinction from chance events, demographic or environmental, becomes unlikely (Crawley 1989). One great irony about biotic invasions is that humans, through cultivation and husbandry, often enhance the likelihood that nonindigenous populations will reach this threshold and become established. This husbandry includes activities that protect small, vulnerable populations from environmental hazards such as drought, flooding, frost, parasites, grazers, and competitors. With prolonged human effort, such crops, flocks, or herds can grow to a size that is not in imminent danger of extinction. In fact,

the population may no longer require cultivation to persist (Lousley 1953). At this point, the population has become naturalized and may eventually become invasive. Thus, humans act to increase the scope and frequency of invasions by serving as both effective dispersal agents and also protectors for immigrant populations, helping favored nonindigenous species beat the odds that defeat most immigrants in a new range (Veltman et al. 1996).

At some point, whether after years or decades, populations of a future invader may proceed into a phase of rapid and accelerating growth, in both numbers and areal spread (Fig. 2). This eruption often occurs rapidly, and there are many first-hand accounts of invasions that proceeded through this phase despite the concerted efforts of the public to control them (Thompson 1922, Elton 1958, Mack 1981). Eventually, an invasion reaches its environmental and geographic limits in the new range, and its populations persist but do not expand.

IDENTIFYING FUTURE INVADERS AND VULNERABLE COMMUNITIES

Identifying future invaders and predicting their likely sites of invasion are of immense scientific and practical interest. Learning to identify invaders in advance would tell us a great deal about how life history traits evolve (Crawley et al. 1996) and how biotic communities are assembled (Lawton 1987). In practical terms, it could reveal the most effective means to prevent future invasions (Reichard and Hamilton 1997). Current hypotheses or generalizations about traits that distinguish both successful invaders and vulnerable communities all concern some extraordinary attributes or circumstances of the species or communities. And all are based on retrospective explanations for past invasions. Evaluation of these generalizations has been difficult because they rely on post hoc observation, correlation, and classification rather than experimentation (Ehrlich 1986, Cronk and Fuller 1995, Holm et al. 1997). Probably no invasions (except some invasions of human parasites) have been tracked closely and quantified from their inception. Furthermore, predictions of future invaders and vulnerable communities are inextricably linked (Crawley 1987). Did a community sustain an invasion because it is intrinsically vulnerable or because the invader possesses extraordinary attributes? Do communities with few current invaders possess intrinsic resistance or have they been reached so far by only weak immigrants? This second issue is confounded by the enormous bias of the opportunity for immigration among different locales (Simberloff 1986, Lonsdale 1999).

Attributes of invaders

Biologists have long sought to explain why so few naturalized species become invaders (Henslow 1879,

as cited in Gray 1879). Intriguingly, some species have invaded several widely separated points on the planet (e.g., *Eichhornia crassipes*, *Imperata cylindrica*, *Parthenium hysterophorus*, *Avena fatua*, *Sturnus vulgaris*, *Rattus rattus*, *Lantana camara*, Long 1981, Brown 1989, Holm et al. 1997), which is the ecological equivalent of winning repeatedly in a high-stakes lottery. Such repeat offenders, or winners, have sparked the obvious question: do they and other successful invasive species share attributes that significantly raise their odds for proliferation in a new range (Ehrlich 1986, Rejmanek and Richardson 1996)?

Many attempts have been made to construct lists of common traits shared by successful invaders (e.g., Wodzicki 1965, Roy 1990). The hope behind such efforts is clear: detect a broad list of traits that, for example, invading insects, aquatic vascular plants, or birds share as a group, then perhaps the identity of future invaders could be predicted from these taxonomic groups. Some invaders do appear to have traits in common, but so far such lists are generally applicable for only a small group of species, and exceptions abound (cf. Crawley 1987, Rejmanek and Richardson 1996).

Relatives of invaders, particularly congeners, seem to be obvious candidates for possession of shared invasive attributes. Taxonomic affinities can indeed identify some potential problems: all but one of the Melastomes naturalized in Hawaii, for instance, are invasive (Wagner et al. 1990). Many of the world's worst invasive plants belong to relatively few families and genera: Asteraceae, Poaceae, *Acacia*, *Mimosa*, *Cyperus* (Heywood 1989, Bingeli 1996, Holm et al. 1997). Rejmanek and Richardson (1996) contend they can successfully predict retrospectively which pines introduced to South Africa are most invasive, based on a list of morphological and ecological characteristics. Furthermore, both Starlings (*Sturnus*) and Crows (*Corvus*) have several invasive, or at least widely naturalized, species (Long 1981). But most biotic invaders have few, if any, similarly aggressive relatives (e.g., *Eichhornia crassipes* is the only *Eichhornia* that is invasive [Barrett 1989]). This lack of correspondence could simply reflect a lack of opportunities for immigration rather than a lack of attributes for invasion (Simberloff 1989). But the circumstantial evidence suggests otherwise: guilt by (taxonomic) association has proven imprecise at predicting invasive potential. Many combinations of traits can apparently spell persistence in a new range, but our ability so far to decipher and quantify these combinations remains poor.

Community vulnerability to invasion

As stated above, attempts to predict relative community vulnerability to invasions have also prompted generalizations, including the following.

Vacant, under- or unutilized niches.—Some com-

TABLE 1. Escape from native parasites and predators often translates into a huge benefit in plant performance, including fitness.

Variable	<i>Chrysanthemoides monilifera</i>		<i>Acacia longifolia</i>	
	Australia	South Africa	Australia	South Africa
Main flowering time	Apr–Aug	Jun–Sep	Aug–Oct	Jul–Sep
Flowers/m ²	1010 ± 170†	840 ± 136	530 ± 30	...
Fruit/flower	6.6 ± 0.3	4.5 ± 0.1	1.1 ± 0.1	...
Green fruit/m ²	6660‡	3755	580	...
Ripe seeds/m ²	4450 ± 750	2160 ± 350	364 ± 70	2923 ± 555
Soil seeds/m ²				
Fragmented	6380 ± 605	2352 ± 20	25 ± 4.2	...
Whole	2475 ± 560	2320 ± 17	7.5 ± 1.0	7600 ± 1440
Viable	2030 ± 460	46 ± 28	5.6 ± 0.8	7370 ± 1400

Notes: *Chrysanthemoides monilifera* and *Acacia longifolia* are native to South Africa and Australia, respectively. Plants of both species display much greater flower and seed production when grown in the other country, benefiting from the escape from native pests and little or no attack by native pests in their new ranges (Weiss and Milton 1984).

† Values are means ± SE.

‡ Calculated.

munities such as tropical oceanic islands appear to be particularly vulnerable to invasions (Elton 1958), although the evidence can be equivocal (Simberloff 1995). The vacant niche hypothesis suggests that island communities and some others are relatively impoverished in numbers of native species and thus cannot provide “biological resistance” to nonindigenous species (sensu Simberloff 1986). However, many potential invaders arriving on islands would find no pollinators, symbionts, or other required associates among the native organisms, a factor that might provide island communities with a different form of resistance to invasion. Yet actual demonstration of vacant niches anywhere has proved difficult (Simberloff 1995).

Escape from biotic constraints.—Many immigrants arrive in new locales as seeds, spores, eggs, or some other resting stage without their native associates, including their usual competitors, predators, grazers, and parasites (Elton 1958, Strong et al. 1984). This “great escape” can translate into a powerful advantage for immigrants. All aspects of performance such as growth, longevity, and fitness can be much greater for species in new ranges (Weiss and Milton 1984, Crawley 1987; Table 1). According to this hypothesis, an invader persists and proliferates not because it possesses a suite of extraordinary traits but rather because it has fortuitously arrived in a new range without virulent or at least debilitating associates. For example, the Australian brushtail possum (*Trichosurus vulpecula*) has become an invader in New Zealand since its introduction 150 years ago (Clout 1999). In New Zealand it has fewer competitors for food and shelter, no native microparasites, and only 14 species of macroparasites, compared with 76 in Australia (Clark et al. 1997). Its population densities in New Zealand forests are 10-fold greater than those prevailing in Australia. Of course, such a successful performance depends on an immigrant not acquiring a new array of competitors,

predators, and parasites in its adopted community. It is probably inevitable on continents that an invader will acquire these foes, especially as it expands its range and comes into contact with a wider group of native species (Strong et al. 1984). The idea of escape from biotic constraints is the most straightforward hypothesis to explain the success of an invader, and also provides the motivation for researchers to search for biological control agents among its enemies in its native range (De Bach and Rosen 1991).

Community species richness.—Elton (1958) proposed that community resistance to invasions increases in proportion to the number of species in the community, its species richness. To Elton, this followed from his hypothesis that communities are more “stable” if they are species-rich. This idea is a variant of the vacant niche hypothesis; i.e., a community with many species is unlikely to have any vacant niches that cannot be defended successfully from an immigrant. On land, however, resistance to plant invasion may correlate more strongly with the architecture of the plant community (specifically, the maintenance of a multitiered plant canopy) than with the actual number of species within the community. For instance, many forest communities have remained resistant to plant invaders as long as the canopy remained intact (Corlett 1992). Here again, exceptions abound (Simberloff 1995).

Disturbance before or upon immigration.—Humans, or the plants and animals they disperse and domesticate, may encourage invasions by causing sudden, radical disturbances in the environment (Harper 1965, Mack 1989). If native species can neither acclimatize nor adapt, the subsequent arrival of preadapted immigrants can lead swiftly to invasions. Such biological consequences can be provoked by fire, floods, agricultural practices, or livestock grazing on land, or by drainage of wetlands or alterations of salinity, and nu-

TABLE 2. Loss of the American chestnut (*Castanea dentata*) through its destruction by the invasive fungus *Endothia parasitica* was swift.

Species	Basal area (dm ² /ha)			Density (no. stems/ha)		
	1934	1941	1953	1934	1941	1953
<i>Castanea dentata</i>	200.53	144.67	3.38	187.82	146.98	16.67
<i>Carya</i> spp.	70.68	60.56	77.82	55.93	62.24	73.81
<i>Quercus prinus</i>	39.43	38.12	53.35	30.71	29.86	25.00
<i>Quercus rubra</i>	36.95	36.39	19.47	29.87	25.45	9.99
<i>Quercus velutina</i>	35.97	40.04	67.44	8.58	13.92	28.81
<i>Aesculus octandra</i>	15.78	16.43	19.02	3.32	3.43	3.56
<i>Quercus alba</i>	15.75	18.50	10.34	10.72	11.41	13.43
<i>Robinia pseudoacacia</i>	14.66	12.86	7.74	14.89	19.62	6.67
<i>Liriodendron tulipifera</i>	11.05	20.83	48.80	38.57	57.39	61.55
<i>Acer rubrum</i>	7.51	9.29	13.99	23.07	22.70	22.86
<i>Betula lenta</i>	7.44	7.78	11.13	6.07	6.07	10.23
<i>Quercus coccinea</i>	5.63	8.16	26.09	1.90	5.71	4.41
Miscellaneous	23.38	27.45	30.15	54.92	62.12	60.86
Total	484.83	441.08	388.72	466.37	466.90	337.85

Notes: Basal area (dm²/ha) and density (no. stems/ha) on Watershed 41 (Coweeta Hydrologic Laboratory, North Carolina in 1934, 1941, and 1953 record original dominance of chestnut in this stand and its destruction within 20 years after arrival of the parasite. Data are for all stems ≥ 1.27 cm (data converted to metric units from Nelson [1955]).

trient levels in streams and lakes. Novel disturbances, or intensification of natural disturbances such as fire, have played a significant role in some of the largest biotic invasions, such as the extensive plant invasions across vast temperate grasslands in Australia and North and South America (Mack 1989, D'Antonio and Vitousek 1992).

The difficulty of predicting any community's vulnerability to an invasion is increased substantially by the bias of immigration, i.e., it is nearly impossible to test critically the relative merits of these hypotheses because of confounding issues, such as the enormous differences among communities in their opportunity to receive immigrants. The likelihood that a community will have received immigrants is influenced largely by its proximity to a seaport or other major point of entry and also the frequency, speed, and mode of dispersal of the immigrants themselves (Simberloff 1989, Williamson 1996, Lonsdale 1999). For example, for more than 300 years an ever-growing commerce has both accidentally and deliberately delivered nonindigenous species to the coasts of South Africa and the northeastern United States. Not surprisingly, the naturalized floras in these regions are very large (Seymour 1969, Richardson et al. 1992). In contrast, some continental interiors, such as Tibet, have minuscule numbers of naturalized plants and animals and few, if any, invaders (Wang 1988). The native biota in such regions may present strong barriers to naturalization and invasion, but isolation alone could explain the lack of invaders.

BIOTIC INVASIONS AS AGENTS OF GLOBAL CHANGE

Human-driven biotic invasions have already caused wholesale alteration of the earth's biota, changing the roles of native species in communities, disrupting evolutionary processes, and causing radical changes in

abundances, including extinctions (Cronk and Fuller 1995, Rhymer and Simberloff 1996). These alterations are collectively a threat to global biodiversity that is second in impact only to the direct destruction of habitat (Walker and Steffen 1997).

Biotic invaders themselves often destroy habitat, for instance by altering siltation rates in estuaries and along shorelines (Bertness 1984, Gray and Benham 1990). In the past, the scope of this direct loss of habitat was local or at most regional. However, with invasions occurring at an unprecedented pace, invaders are collectively altering global ecosystem processes (Vitousek et al. 1996). Furthermore, the growing economic toll caused by invasions is not limited by geographic or political boundaries (U.S. Congress 1993, Sandlund et al. 1996). Invaders are by any criteria major agents of global change today. We provide below only a brief sketch of the range of effects that biotic invaders cause to biodiversity and ecological processes.

Population-level effects

Invasions by disease-causing organisms can severely impact native species. The American chestnut (*Castanea dentata*) once dominated many forests in the eastern United States, especially in the Appalachian foothills (Braun 1950), until the Asian chestnut blight fungus arrived in New York City on nursery stock early in this century. Within a few decades, the blight had spread throughout the eastern third of the United States, destroying almost all American chestnuts within its native range (Roane et al. 1986) (Table 2). The mosquito *Culex quinquefasciatus* that carries the avian malaria parasite was inadvertently introduced to the Hawaiian Islands in 1826. The parasite itself arrived subsequently, along with the plethora of Eurasian birds that now dominate the Hawaiian lowlands. With avian malaria

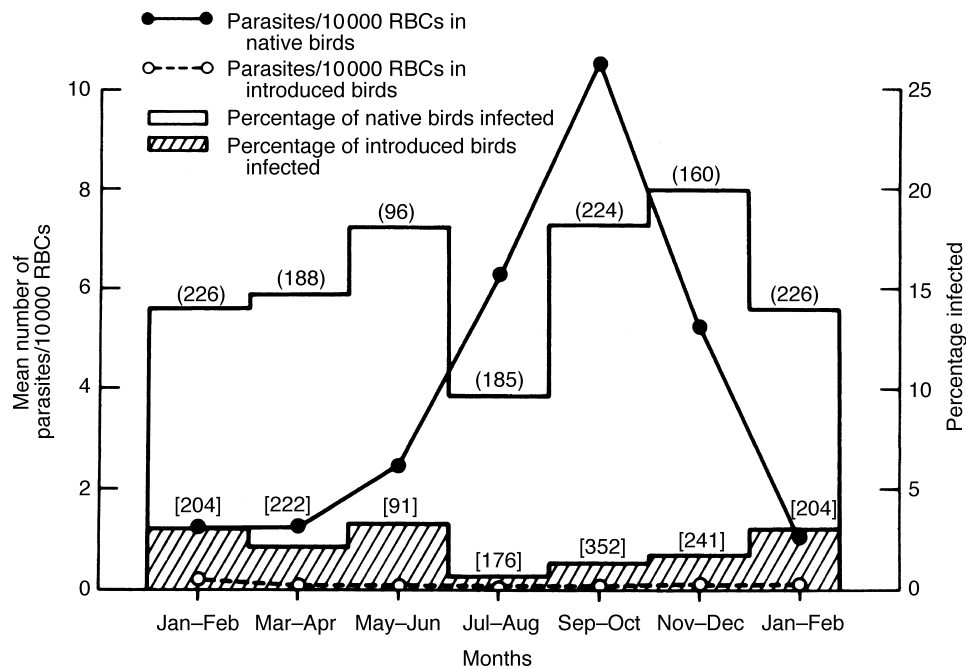


FIG. 3. Percentage levels of native and nonindigenous birds on Mauna Loa, Hawaii, infected with avian malaria, 1978–1979 and mean numbers of parasites per 10 000 RBCs. As a result of the native birds' greater susceptibility, they were largely restricted to higher elevations. Numbers in brackets or parentheses are sample sizes (Van Riper et al. 1986). RBC = red blood cells.

rampant in the lowlands, the Eurasian invaders, which are at least somewhat resistant to it, have excluded native Hawaiian birds, which are highly susceptible to the disease (van Riper et al. 1986; Fig. 3).

Predation and grazing by invaders can also devastate native species. The predatory Nile perch (*Lates nilotica*), which was introduced into Africa's Lake Victoria, has already eliminated or gravely threatens more than 200 of the 300 to 500 species of the great evolutionary radiation of native cichlid fishes (Goldschmidt 1996). Feral and domestic cats have been transported to every part of the world and have become devastating predators of small mammals and ground-nesting or flightless birds. On many oceanic islands, feral cats have depleted breeding populations of seabirds and endemic land birds. In New Zealand, cats have been implicated in the extinction of at least six species of endemic birds, as well as some 70 populations of island birds (King 1985). In Australia, cat predation takes its biggest toll on small native mammals. Cats are strongly implicated in 19th century extinctions of at least six species of native Australian marsupials (*Pseudomys* and *Notomys*) (Dickman 1996). The brown tree snake (*Boiga irregularis*), introduced to Guam in the late 1940s from the Admiralty Islands (Rodda et al. 1992), has already virtually eliminated all forest birds in Guam (Savidge 1987). Goats introduced to St. Helena Island in 1513 almost certainly extinguished more than 50 endemic plant species, although only seven were scientifically

described before their extinction (Groombridge 1992). Invaders still extract a severe toll on St. Helena. A South American scale insect (*Orthezia insignis*) has recently threatened the survival of endemic plants, including the now rare native tree, *Commidendrum robustum*. Two years after the scale infestation began in 1993, at least 25% of the 2000 remaining trees had been killed (Booth et al. 1995).

Nonindigenous species may also compete with natives for resources. The North American gray squirrel (*Sciurus carolinensis*) is replacing the native red squirrel (*S. vulgaris*) in Britain by foraging more efficiently (Williamson 1996). The serial invasion of New Zealand's *Nothofagus* forests by two wasp species has harmed native fauna, including both invertebrates that are preyed on by wasps and native birds that experience competition for resources (Clout 1999). For instance, the threatened Kaka (*Nestor meridionalis*), a forest parrot, forages on honeydew produced by a native scale insect. But >95% of this resource is now claimed by invasive wasps during the autumn peak of wasp density, and as a result the parrots abandon the *Nothofagus* forests during this season (Beggs and Wilson 1991). The native biota of the Galapagos Islands is threatened by goats and donkeys, not only because of their grazing but because they trample the breeding sites of tortoises and land iguanas (Bensted-Smith 1998). Invasive plants have diverse means of competing with natives. Usurping light and water are probably the most com-

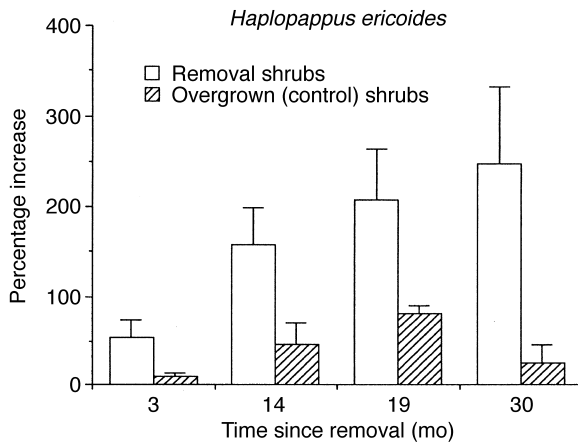


FIG. 4. *Carpobrotus edulis*, a sprawling perennial plant, invades California coastal communities. It overtops native species, such as *Haplopappus ericoides*, and competes aggressively for soil water. Its removal coincides with a marked increase in canopy area of *H. ericoides*; values represent change as a percentage of initial canopy area. Error bars are ± 1 SE (D'Antonio and Mahall 1991).

mon tactics. For example, the succulent mat-former, *Carpobrotus edulis*, pervades the same shallow rooting zone as native shrubs in California coastal communities. Its removal coincides with improved water availability for the natives, strongly suggesting that the invasive *C. edulis* usurps water that would otherwise be available for native plants' growth (D'Antonio and Mahall 1991; Fig. 4).

Interference competition by invasive species is even more easily demonstrated. For example, several widely introduced ant species (the red fire ant [*Solenopsis invicta*], the Argentine ant [*Linepithema humile*], and the big-headed ant [*Pheidole megacephala*]) all devastate large fractions of native ant communities by aggression (references in Williams 1994; Fig. 5). Although the evidence is often equivocal for allelopathy, the widely introduced agricultural pest *Agropyron repens* is one of the few species that likely interferes with competitors through release of phytotoxins (Welbank 1960).

Invasive species can also eliminate natives by mating with them, a particular danger when the native species is rare. For example, hybridization with the introduced North American Mallard (*Anas platyrhynchos*) threatens the existence, at least as distinct species, of both the New Zealand Gray Duck (*Anas superciliosa*) and the Hawaiian Duck (*A. wyvilliana*; references in Rhymer and Simberloff 1996). Hybridization between a non-indigenous species and a native one can even produce a new invasive species. For example, North American cordgrass (*Spartina alterniflora*), carried in shipping ballast to southern England, hybridized occasionally with British native cordgrass (*S. maritima*). These hybrid individuals were sterile, but eventually one underwent a doubling of chromosome number to produce

a fertile, highly invasive species, *S. anglica* (Thompson 1991). Hybridization can threaten a native species even when the hybrids do not succeed, simply because cross-breeding reduces the number of new offspring added to the species' own population. For example, females of the European mink (*Mustela lutreola*), already gravely threatened by habitat deterioration, hybridize with males of introduced North American mink (*M. vison*). Embryos are invariably aborted, but the wastage of eggs exacerbates the decline of the native species (Rozhnov 1993).

Species can evolve after introduction to a new range. The tropical alga, *Caulerpa taxifolia*, evolved tolerance for colder temperatures while it was growing at the aquarium of the Stuttgart Zoo and other public and private aquaria in Europe. Since then it has escaped into the northwest Mediterranean, and its new tolerance of winter temperatures has permitted it to blanket vast stretches of the seafloor, threatening nearshore marine communities (Meinesz 1999). Evolution can also

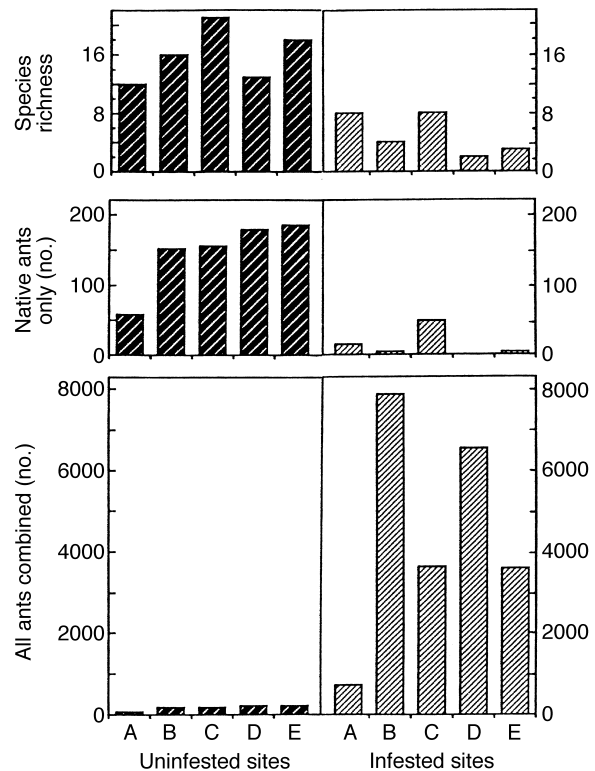


FIG. 5. Invasion of Brazilian fire ants, *Solenopsis invicta*, into woodlands and grasslands in central Texas causes a radical change in the density and species composition of the native ant fauna, as reflected in pitfall trap records. Species richness and numbers of native ant workers decline sharply, while the invader's populations are several orders of magnitude greater than all ants in unfested sites. Note the much larger scale on the bottom graph, showing numbers of all ants combined. All values were calculated with site pitfall trap totals summed across May, July, and October 1987 (Porter and Savignano 1990).

change potential impacts in subtler ways. *Bathyplectes curculionis*, an ichneumonid parasitic wasp imported to the United States to control the alfalfa weevil (*Hypera postica*) was originally ineffective against the Egyptian alfalfa weevil, *Hypera brunneipennis*. Dissections showed that 35–40% of its eggs were destroyed by the immune response of the larval weevil. Samples taken fifteen years later showed only 5% egg loss (Messenger and van den Bosch 1971).

Community- and ecosystem-level effects

The biggest ecological threat posed by invasive species is the disruption of entire ecosystems, often by invasive plants that replace natives. For example, the Australian paperbark tree (*Melaleuca quinquenervia*), which at one time increased its range in south Florida by >20 ha per day, replaces cypress, sawgrass, and other native species. It now covers about 160 000 ha, often in dense stands that exclude virtually all other vegetation. It provides poor habitat for many native animals, uses huge amounts of water, and intensifies the fire regime (Schmitz et al. 1997). Similarly, *Mimosa pigra* has transformed 80 000 ha of tropical wetland habitat in northern Australia into monotonous tall shrubland (Braithwaite et al. 1989), excluding native waterbirds. The South American shrub, *Chromolaena odorata* or Siam weed, is not only an aggressive invader in both Asia and Africa, suppressing the regeneration of primary forest trees, but also provides feeding niches that can sustain other pests (Boppré et al. 1992). Another highly invasive neotropical shrub, *Lantana camara*, serves as habitat for the normally stream-dwelling tsetse fly in East Africa, increasing the incidence of sleeping sickness in both wild and domesticated animals, as well as in humans (Greathead 1968).

Many invasive species wreak havoc on ecosystems by fostering more frequent or intense fires, to which key native species are not adapted. *Melaleuca quinquenervia* has this effect in Florida (Schmitz et al. 1997), as do numerous invasive grasses worldwide (D'Antonio and Vitousek 1992). In general, grasses produce a great deal of flammable standing dead material, they can dry out rapidly, and many resprout quickly after fires (D'Antonio and Vitousek 1992).

An invasion of Hawaii Volcanoes National Park by a small tree, *Myrica faya*, native to the Canary Islands, is transforming an entire ecosystem because the invader is able to fix nitrogen and increase supplies of this nutrient in the nitrogen-poor volcanic soils at a rate 90-fold greater than native plants (Vitousek and Walker 1989; Table 3). Many other nonindigenous plants in Hawaii are able to enter only sites with relatively fertile soils, so *M. faya* paves the way for further invasions, raising the threat of wholesale changes in these plant communities (Vitousek et al. 1987). *Myrica faya* also attracts the introduced Japanese White-eye (*Zosterops japonica*); the White-eye disperses *Myrica* seeds (Vi-

TABLE 3. *Myrica faya*, an invasive nitrogen-fixing tree in Hawaii, radically increases the local nitrogen budget and thus facilitates the entry of other nonindigenous species into native communities.

Source	N input (kg/ha)	
	LB	UB
Fixation by <i>Myrica faya</i>	18.5	0.2
Native N fixation		
Lichens	0.02	0.06
Litter	0.12	0.16
Decaying wood	0.05	0.03
Precipitation		
NH ₄ -N + NO ₃ -N	1.0	1.0
Organic N	2.8	2.8
Total inputs	22.5	4.2

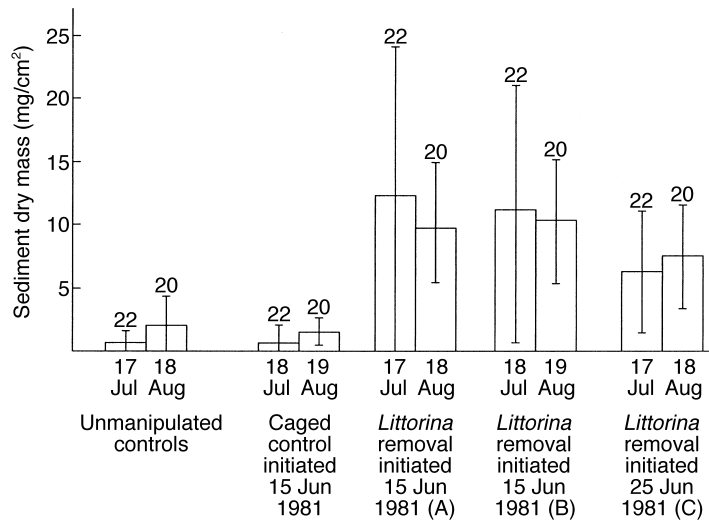
Note: Annual nitrogen inputs are compared for two sites: LB, in which *M. faya* density was >1000 plants/ha by 1987; and UB, in which *M. faya* had only recently arrived (Vitousek and Walker 1989).

tousek and Walker 1989) and is believed to be a competitor of several native bird species (Mountainspring and Scott 1985).

Ecosystem transformations wrought by invaders have been so complete in some locales that even the landscape itself has been profoundly altered. "The Bluegrass Country" of Kentucky invokes images for most Americans of a pastoral, even pristine, setting. But bluegrass is *Poa pratensis*, a Eurasian invader that supplanted the region's original vegetation, an extensive open forest and savanna with *Elymus* spp. and possibly *Arundinaria gigantea* in the understory (Daubenmire 1978), after European settlement and land clearing. The European periwinkle (*Littorina littorea*), introduced to Nova Scotia around 1840, has transformed many of the coastal inlets along the northeast coast of North America from mudflats and salt marshes to a rocky shore (Bertness 1984; Fig. 6). Similar wholesale transformations of the landscape have occurred elsewhere, including the conversion of the Florida Everglades from a seasonally flooded marsh to a fire-prone forest of invasive trees (Bodley et al. 1994) and the invasion of the fynbos in South Africa's Cape Province by eucalypts, pines, *Acacia*, and *Hakea* spp. (van Wilgen et al. 1996). Heavy water use by these invasive trees in South Africa has led to major water losses (estimated at 3×10^9 m³/y, Anonymous 1997b), and many rivers now do not flow at all or flow only infrequently. This change has in turn reduced agricultural production and also threatened the extinction of many endemic plant species from the Cape flora (van Wilgen et al. 1996).

Our best estimate is that, left unchecked, the current pace and extent of invasions will influence other agents of global change, principally the alteration of greenhouse gases in the atmosphere, in an unpredictable but profound manner (Mack 1996). The current transfor-

FIG. 6. *Littorina littorea* (European periwinkle) has greatly increased the extent of rocky shoreline along New England and the Canadian Maritime coast through its grazing on marine plants that once induced siltation and mud accumulation. Its removal and exclusion from areas caused a rapid resumption in sedimentation with accompanying algal colonization. Error bars show ± 1 SD; sample sizes of sites appear over each bar (Bertness 1984).



mation of ecosystems in the Amazon basin through the burning of forests and their replacement with African grasses provides one of the most ominous examples. For example, in Brazil the conversion of diverse forest communities into croplands and pastures has often involved the deliberate sowing of palatable African grasses (*Melinis minutiflora*, *Hyparrhenia rufa*, *Panicum* spp., and *Rhynchelytrum repens*) (Eiten and Goodland 1979). The spread and proliferation of these grasses has been fostered by fire. By 1991 cleared forest sites that largely support grass-dominated communities were estimated to cover 426 000 km² in Brazil alone (Fearnside 1993); much more of the 4 × 10⁶ km² of the multilayered forest in the Amazon basin in Brazil is at risk of similar conversion.

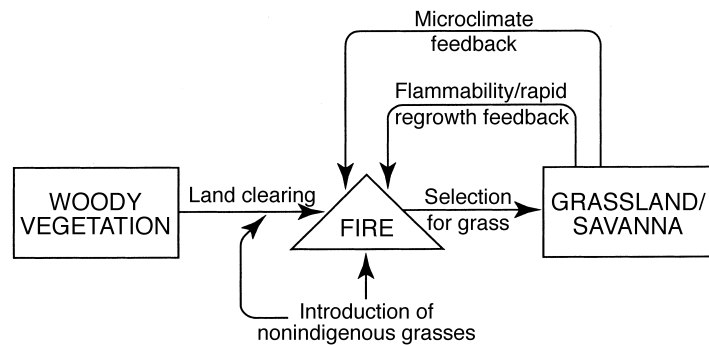
These extensive human-driven grass invasions could not only alter ecosystem-level properties in Brazil but also have repercussions worldwide (Vitousek et al. 1996). Perhaps most significant is the fact that grasslands contain much less plant biomass than the native forests and thus sequester less carbon (Kaufmann et al. 1995, Kaufmann et al. 1998). Given the extent of the neotropical forests, continuing conversions to grasslands could exacerbate the buildup of carbon dioxide

in the atmosphere, potentially influencing global climate. Less evapotranspiration from grasslands compared to tropical forest (Shukla et al. 1990) could also translate into greater convective heat loss and increases in air temperature (Walters 1979). Although fire and other agents of land-clearing initiate these changes in the Amazon watershed, the persistence of invasive grasses thereafter limits any natural recolonization of cleared areas by native forest species. Thus, invasive African grasses are having a ratchet-like effect in the Amazon watershed: as more of the native vegetation is converted to pasture, these grasses prevent recolonization and succession by native species (Fig. 7).

Economic consequences

Attempts to arouse public and governmental support for the prevention or control of invasions often fail because of a lack of understanding of the inextricable link between nature and economy. But the threats biotic invasions pose to biodiversity and to ecosystem-level processes translate directly into economic consequences such as losses in crops, fisheries, forestry, and grazing capacity. Yet no other aspect of the study of biotic invasions is as poorly explored and quantified. Al-

FIG. 7. Invasion of African grasses in the Amazon Basin could eventually cause the permanent conversion of this vast forested carbon sink into grassland or savanna-like areas. As depicted schematically, fire-initiated land clearing allows the entry of these grasses. The flammability of their abundant litter rapidly fosters their persistence at the expense of native woody species. This ratchet-like conversion across such a huge area holds important implications for ecosystem alteration at a global scale (D'Antonio and Vitousek 1992).



though there are ample anecdotal examples of local and even regional costs of invaders, we consistently lack clear, comprehensive information on these costs at national and especially global levels.

Biotic invasions cause two main categories of economic impact. First is the loss in potential economic output: i.e., losses in crop production and reductions in domesticated animal and fisheries survival, fitness, and production. Second is the direct cost of combating invasions, including all forms of quarantine, control, and eradication (U.S. Congress 1993). A third category, beyond the scope of this report, would emphasize the costs of combating invasive species that are threats to human health, either as direct agents of disease or as vectors or carriers of disease-causing parasites.

These costs form a hidden but onerous "tax" on many goods and services. Tallying these costs, however, remains a formidable task. Pimentel et al. (2000) attempted recently to tabulate the annual cost of all nonindigenous species in the United States. They estimate that nonindigenous weeds in crops alone cost U.S. agriculture ~\$27 billion per year, based on a potential crop value of ~\$267 billion. Loss of forage and the cost of herbicides applied to weeds in rangelands, pastures, and lawns cause a further \$6 billion in losses each year. When they combined these direct losses with indirect costs for activities such as quarantine, the total cost of all nonindigenous species (plants, animals, microorganisms) exceeded \$138 billion per year. By any standard, such costs are a formidable loss, even for a productive industrialized society such as the United States.

These estimates illustrate the preliminary level of our current understanding of the economics of invasions. One solution would be a more frequent application of economic tools such as cost-benefit analyses when considering proposals to import species for perceived economic benefit (Naylor 1996, Pannell 1999). When it comes to future movements of species, society needs to be able to consider results from the types of analysis economists already provide for other projects with potential environmental consequences, such as construction of hydroelectric dams, canals, and airports. We predict that cost-benefit analysis of many deliberately introduced invaders would demonstrate forcefully that their costs to society swamp any realized or perceived benefits.

PREVENTION AND CONTROL OF BIOTIC INVASIONS

The consequences of biotic invasions are often so profound that they must be curbed and new invasions prevented. This section is divided into two parts: first, efforts to prevent the opportunity for invasions by prohibiting the entry of nonindigenous species into a new range; and second, concepts for curbing the spread and impact of nonindigenous species, including invaders, once they have established in a new range.

Preventing entry of nonindigenous species

The use of quarantine, which is intended to prohibit organisms from entering a new range, has a long history in combating human parasites (McNeill 1976). Rarely is the saying "an ounce of prevention is worth a pound of cure" so applicable as with biotic invasions. Most invasions begin with the arrival of a small number of individuals (Simberloff 1986, Mack 1995), and the costs of excluding these is usually trivial compared to the cost and effort of later control after populations have grown and established.

The ability of a nation to restrict the movement of biotic invaders across its borders is ostensibly governed by international treaties, key among them being the Agreement on the Application of Sanitary and Phytosanitary Measures (SPS) (Anonymous 1994). Under this agreement members of the World Trade Organization (WTO) can restrict movement of species that may pose a threat to human, animal, or plant life (Anonymous 1994). The International Plant Protection Convention (IPPC) of 1951 deals with quarantine against crop pests (Jenkins 1996), and the IPPC Secretariat also coordinates phytosanitary standards (Anonymous 1994). The SPS agreement requires WTO members to base any SPS measures on internationally agreed guidelines (see Anonymous 1994).

Unfortunately, neither the specific wording, current interpretation, nor implementation of these agreements provides totally effective control against biotic invaders. Nations may give variances or exceptions based on politico-economic considerations that outweigh biological concerns. Even if a nation attempts to ban importation of a species, its efforts may fall to international judgment if the WTO, in its regulatory capacity, rules that the ban is an unlawful or protectionist trade barrier rather than a legitimate attempt to exclude pests (Jenkins 1996). Thus, environmental concerns and politico-economic interests may clash.

Within these international guidelines, some countries, including Australia and the United States, have imposed quarantine controls that take an "innocent until proven guilty" approach, e.g., they have allowed entry of any nonindigenous species that are not known to be harmful. This approach has been attacked from two sides: some want to liberalize trade, remove non-tariff trade barriers, and ease quarantine controls; opponents argue that the precautionary principle should apply and that a "guilty until proven innocent" approach should be used to tighten current quarantine protocols (Panetta et al. 1994).

The current U.S. approach is clearly inadequate to stem the tide of entering nonindigenous organisms, and the U. S. Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) is considering policy changes (Reichard and Hamilton 1997). These might involve conducting risk assessments that would

estimate the invasive potential of a species proposed for import (Ruesink et al. 1995). In 1997, the Australian Quarantine Inspection Service (AQIS) adopted such a risk assessment system for screening new plant imports based on their biological attributes and the consequent risk of invasiveness that they pose.

As described earlier, attempts to predict from biological attributes which species will become invasive have had very mixed success (Perrins et al. 1992). Debate continues between those who maintain that quarantine risk assessment may be achievable (Pheloung 1995, Rejmanek and Richardson 1996, Reichard and Hamilton 1997) and those who argue that prediction of invasiveness will always be extremely difficult (Simberloff 1989, Lonsdale 1994, Williamson 1996). Clearly, much research on prediction remains to be done. If risk assessment screening procedures are to be applied as part of a government policy, however, more must be considered than predictive accuracy. The low *base rate* at which species become naturalized as well as the base rate for becoming invaders means that the predictive power of any risk assessment must be very high to identify invaders reliably (Smith et al. 1999). As a consequence, screening systems are likely to produce high rates of false positives (C. S. Smith, *unpublished data*).

In after-the-fact assessments of previously introduced plants, the screening system now adopted by AQIS had an accuracy of ~85% (Pheloung 1995). The AQIS system rejects or recommends for further evaluation roughly 30% of the species proposed for import (Pheloung 1999). It is likely that the vast majority of these are "false positives" that would not have become invasive (Smith et al. 1999). But such an exclusionary policy risks conflict between environmentalists and commodity groups, such as horticulturists, who advocate the liberal introduction of species. Whether this degree of restriction on trade can be sustained remains to be seen; globally, society is unlikely ever to prohibit liberal movement of plants and animals in commerce. Thus, the challenge is to identify the few potentially harmful immigrants among an increasing throng of innocuous entrants.

Eradication

Eradication of a nonindigenous species is sometimes feasible, particularly if it is detected early and resources can be applied quickly (Simberloff 1997). Usually, however, there is insufficient ongoing monitoring, particularly in natural areas, to detect an infestation soon after it occurs. Many regulatory agencies tend to ignore nonindigenous species, feeling that attempts at control are not worth the bother and expense until one becomes widespread and invasive. Unfortunately, by that time eradication is probably not an option (Simberloff 1997). This problem of getting agencies to take nonindigenous species seriously is exacerbated by the pro-

longed lag times between establishment of some immigrant species and their emergence as invaders.

Nevertheless, some potentially damaging nonindigenous species have been eradicated. For example, an infestation of the Asian citrus blackfly (*Aleurocanthus woglumi*) on Key West in the Florida Keys was eradicated between 1934 and 1937 (Hoelmer and Grace 1989). This eradication project had many advantages: there was no highway to the mainland at the time, and the only railroad bridge was destroyed by a hurricane in 1935. Insularity also featured prominently in an eradication campaign against the screwworm fly (*Cochliomyia hominivorax*) by the release of sterile males. Apparent success of this approach on Sanibel Island, Florida led to a similar trial on Curacao, and eradication in that trial led to widespread release of sterile males throughout the southeastern United States (Dahlsten 1986).

The giant African snail (*Achatina fulica*), a major pest of agriculture in many parts of its introduced range in Asia and the Pacific, was eradicated in sustained campaigns against established but fairly localized populations in south Florida (Simberloff 1997) and Queensland, Australia (Colman 1978). Local populations of nonindigenous freshwater fishes are often eradicated (Courtenay 1997), and New Zealand has eradicated various combinations of twelve mammal species (ranging from rodents through feral domestic animals) from many islands of up to 2000 ha (Veitch and Bell 1990). A few nonindigenous but not yet invasive plant populations have been completely eradicated; these were all from very small areas, however. For example, Asian common wild rice (*Oryza rufipogon*) was eliminated from 0.1 ha of the Everglades National Park (Simberloff 1997) and all Japanese dodder (*Cuscuta japonica*) was apparently destroyed in a 1-ha infestation in Clemson, South Carolina (Westbrooks 1993; R. Westbrooks, *personal communication*).

Some eradication efforts have been successful against widespread species. For example, bacterial citrus canker (*Xanthomonas campestris* pv. *citri*) was eradicated from a broad swath of the southeastern United States in the early 20th century (Merrill 1989), and a 50-year campaign succeeded in eliminating the South American nutria (*Myocastor coypus*) from Britain (Gosling 1989).

In all these instances, three key factors contributed to success. First, particular aspects of the biology of the target species suggested that the means employed might be effective. For example, the host specificity and poor dispersal ability of the citrus canker were crucial to a successful eradication strategy. Second, sufficient resources were devoted for a long enough time. If funding is cut as soon as the immediate threat of an economic impact lessens, eradication is impossible. Third, there was widespread support both from the relevant agencies and the public. Thus, for example,

people rigorously heeded quarantines and various sanitary measures.

Even when complete eradication fails, the effort may well have proven cost effective and prevented substantial ecological damage. For example, a long campaign to eradicate witchweed (*Striga asiatica*), an African root parasite of several crops in the Carolinas, has reduced the infestation from 162 000 to 6 000 ha (Westbrooks 1998). The methods employed—herbicides, soil fumigants to kill seeds, and regulation of seed-contaminated crops and machinery—would have been used anyway simply to control this invader. The control is successful even if eradication is not complete.

Other large eradication projects, however, have been so unsuccessful that they have engendered public skepticism about the entire endeavor and have, in some instances, worsened the problem. The long campaign to eradicate imported fire ants (*Solenopsis invicta* and *S. richteri*) from the southern United States has been labeled by E. O. Wilson as “the Vietnam of entomology” (Brody 1975) and was a \$200 million disaster (Davidson and Stone 1989). Not only did fire ants reinvade areas cleared of ants by insecticides, but they also returned faster than many native ant species. The introduced range of fire ants expanded several-fold during the 20-year campaign, and enough was known at the time about the biology of these ants that the outcome could have been predicted (Davidson and Stone 1989).

Maintenance control

If eradication fails, the goal becomes “maintenance control” of a species at acceptable levels (Schardt 1997). Three main approaches, applied singly or in various combinations, are widely used: chemical, mechanical, and biological control.

Chemical control probably remains the chief tool in combating nonindigenous pests in agriculture. Chemical controls, unfortunately, have too often created health hazards for humans and nontarget species. For example, problems associated with DDT are well known. But the frequent evolution of pest resistance (National Research Council 1986), the high cost, and the necessity of repeated applications often make continued chemical control impossible. If the goal were to control an invasive species in a vast natural area, the cost of chemical methods alone would be prohibitive. Even when there is no firm evidence of a human health risk, massive use of chemicals over heavily populated areas inevitably generates enormous public opposition, as demonstrated by the heated responses to recent aerial spray campaigns using malathion against the medfly in California (Carey 1992).

Chemical control of plant parasites has a mixed record, depending on the parasite and the scale of required protection. In native forests in Australia, broadscale

chemical control of the root fungus *Phytophthora cinnamomi* was at best only temporarily effective, while injection of individual trees was deemed too expensive (Weste and Marks 1987). The history of controlling coffee rust (*Hemileia vastatrix*) in Latin America is emblematic of the frustration of attempting to control invasive plant pathogens. Repeatedly, each affected coffee-growing country applied a barrage of fungicides, initially attempting to eradicate the parasite and then attempting to contain it (Hill and Waller 1982; J. M. Waller, *personal communication*).

Mechanical methods of controlling nonindigenous organisms are sometimes effective and usually do not engender public criticism. Sometimes they can even be used to generate public interest in and support for control of invasive species. In Florida's Blowing Rocks Preserve, volunteers helped remove Australian pine (*Casuarina equisetifolia*), Brazilian pepper (*Schinus terebinthifolius*), and other invasive plants and to plant more than 60 000 individuals of 85 native species (Randall et al. 1997). Hand-picking of giant African snails was a key component of the successful eradication campaigns in Florida and Queensland (Simberloff 1997 and references therein). However, equipment expenses, the difficulty of actually finding the target organisms, and the geographic scale of some nonindigenous species infestations frequently render mechanical control impossible.

Hunting is often cited as an effective method of maintenance control of nonindigenous animals, and hunting and trapping were crucial in the successful eradication of the nutria from Britain. In the Galápagos Islands, park officials have a long-established campaign to eradicate nonindigenous mammals, and over the past 30 years goats have been eliminated from five islands (Ospina 1998). By contrast, recreational hunting alone is unlikely to serve as an effective control on an invasive mammal. In New Zealand, hunting of Australian brushtail possums was encouraged from 1951 to 1961 through a bounty system and harvesting of animals for pelts. More than 1 million animals each year were shot or trapped in the late 1950s. Nevertheless, the possum continued to spread (McDowall 1994). Recreational hunting of introduced red deer (*Cervus elaphus*) in New Zealand has also generally failed to reduce densities enough to speed regeneration of native forests. For both possums and red deer, widespread control is now conducted primarily by aerial application of poison baits, which has its own set of problems, including lack of widespread public acceptance (Clout 1999).

Problems with both chemical and mechanical controls have focused attention on biological control—the introduction of a natural enemy of an invasive species. In a sense, this is a planned invasion. It aims to establish in the new range at least part of the biotic control the target species experiences in its native range. Some

biological control projects have succeeded in containing very widespread, damaging infestations at acceptable levels with minimal costs. Examples include the well-known control of invasive prickly pear cactus (*Opuntia inermis* and *O. stricta*) in Australia by the moth *Cactoblastis cactorum* from Argentina (Osmond and Monro 1981); control of South American alligator weed (*Alternanthera phyloxeroides*) in Florida and Georgia by a flea beetle (Center et al. 1997), and control of the South American cassava mealybug (*Phenacoccus manihoti*) in Africa by a South American encyrtid wasp (Odour 1996). In each of these cases, the natural enemy has controlled the pest in perpetuity, without further human intervention. When the pest increases in numbers, the natural enemy increases correspondingly, causing the pest to decline, which entrains a decline in the natural enemy. Neither player is eliminated; neither becomes common.

Caveats on biological control

Biological control has recently been critically scrutinized on the grounds that nontarget species, some of them the focus of conservation efforts, have been attacked and even driven to extinction by nonindigenous biocontrol agents (Howarth 1991, Simberloff and Stiling 1996). For example, the widespread introduction of a New World predatory snail, *Euglandina rosea*, to control the giant African snail led to extinction of many endemic snail species in the Hawaiian and Society islands (Civeyrel and Simberloff 1996 and references therein). In these cases, the predators attacked many prey species, thus preventing a mutual population control from developing between the predator and any single prey species.

Insect biological control agents that have been subjected to rigorous host-specificity testing have nevertheless been known to attack nontarget species. For example, a Eurasian weevil, *Rhinocyllus conicus*, introduced to North America to control invasive musk thistle (*Carduus nutans*), is now attacking native non-pest thistles. These natives include a federally listed endangered species and narrowly restricted endemic species in at least two Nature Conservancy refuges, three national parks, and state lands (Federal Register 1997, Louda et al. 1997). Controversy about the extent of such problems focuses primarily on two issues: whether there is sufficient monitoring to detect such nontarget impacts, and the likelihood that an introduced biological control agent will evolve to attack new hosts. However, the ability of *R. conicus* to attack these native species had been detected before its release; poor legislation, rather than an incomplete assessment precipitated the controversy (J. Waage, *personal communication*). The fact that biological control agents can disperse and evolve, as can any other species introduced to a new range, implies that their preliminary testing

should be extensive and conducted under extremely secure circumstances.

Exclusion and control: socioeconomic issues

The difficulties of curbing biotic invasions illustrate the problem of implementing scientifically based recommendations in an arena in which diverse segments of society all have important stakes. At every level of prevention and control, the thorny issues are as likely to be socioeconomic as scientific.

A persistent problem with current methods of exclusion and control is that they largely assume goodwill and cooperation on the part of all citizens. For widely varying reasons, large segments of entire industries are committed to the introduction, at least in controlled settings, of many nonindigenous species and are skeptical of arguments that they will escape and/or be problematic if they do escape. Thus, there is often organized opposition to proposals to stiffen regulations relating to introduction, and there is also frequent careless or even willful disregard of existing laws.

The horticulture industry is often in the vanguard of opposition to tight control of nonindigenous species. It is a diverse multibillion dollar industry with importers running the gamut from small, family operations specializing in a few species to large corporations importing hundreds of taxonomically diverse species. At one extreme, some horticulturists generate publications and websites scoffing at the very existence of ecological problems with nonindigenous species. On the other hand, many plant importers recognize the dangers and at least support quarantine measures and limited blacklists of species known to be invasive. However, as a whole, through trade associations and as individuals, horticulturists attempt to influence the political process as it concerns regulation of nonindigenous species (Sray 1997). Furthermore, individuals who purchase plants from importers are generally under far less legal obligation and undergo little scrutiny in their use of these plants.

Horticulturists have also been at least loosely allied with other interest groups that desire quite unfettered access to the world's flora. State departments of transportation, charged with landscaping highways, as well as the U.S. Natural Resource Conservation Service, constituted to battle erosion, have traditionally favored nonindigenous species for these purposes (McArthur et al. 1990). At least some state departments of transportation are now moving toward use of native plants (e.g., Caster 1994), but a long history of interaction between these departments and private horticulturists slows this process.

Agricultural interests and their regulatory agencies have had a schizophrenic relationship with nonindigenous species. On the one hand, they promote the importation of useful and profitable crop plants and livestock. On the other, they hope to control the influx of

parasites, insect pests, and agricultural weeds. For example, the thistle weevil discussed above as a biocontrol agent that attacks nontarget species was introduced to North America by Agriculture Canada and spread in the United States by the U.S. Department of Agriculture and various state agricultural agencies. The Hawaii Department of Agriculture introduced the carnivorous snail *Euglandina rosea* to the Hawaiian Islands to control the giant African snail (Davis and Butler 1964).

The pet industry is also heavily invested in nonindigenous species. As with the horticulture industry, it encompasses a tremendous range of operations in terms of size, scope, and degree and nature of specialization, and there is no monolithic stance toward threats posed by nonindigenous species and the prospect of rigorous control. As with horticulturists, through the political and publicity activities of individuals and trade organizations, the general attitude of the pet industry toward strict regulation of introductions has ranged from skepticism to outright hostility (U.S. Congress 1993, Bullington 1997).

Many domesticated or pet animals have escaped from importers and breeders (for example, when fires or storms destroyed cages), and some have become invasive. In Britain, escapees from fur farms established a feral population of nutria (Lever 1979), which became the target of a lengthy eradication campaign noted above. Sometimes, pet dealers or owners deliberately release animals. For example, some fishes are deliberately released by aquarists (Courtenay 1997). Again, as with horticulturists, once a pet is sold, the dealer has no subsequent control over the owner's actions, and the owner may be less likely than the dealer to obey formal regulations.

Controversies over the management of feral horses in both the United States and New Zealand illustrate the conflicts that readily arise between various segments of society about some widely appreciated feral domestic animals. In both countries feral horses pose documented threats to native species and ecosystems. Yet some groups contend the horses that escaped from Spanish explorers in North America ~500 years ago "belong" in the West, merely serving as replacements for native equids that became extinct on the continent ~10 000 years ago. In New Zealand, however, there were no native land mammals, except for bats, before introductions by people began over the past 800 years. Horses were introduced to New Zealand <200 years ago.

In New Zealand, feral horses have occupied the central North Island since the 1870s. Land development and hunting progressively reduced both their numbers and range; a 1979 census revealed only about 174 animals. By 1981, however, public lobbying resulted in creation of a 70 000-ha protected area as the herd's core range. With protection, horses expanded their range and

increased to 1576 animals by 1994, essentially doubling their population every four years (New Zealand Department of Conservation 1995). In response to damage in native ecosystems caused by this rapidly growing population, the New Zealand Department of Conservation (1995) recommended removal of the protected area, eradication of horses from 70% of their range, and management to retain a herd of about 500 animals in the remaining range. The management plan, which included shooting horses, provoked intense public protest. This outcry eventually resulted in the overturning of a scientifically based management plan and a 1997 decision to round up as many horses as possible for sale. Sale of several hundred horses duly took place, but the long-term fate of the growing herd remains unresolved.

The impasse in New Zealand over feral horse control has been mirrored in Nevada, where an intense dispute has raged between land managers and pro-horse activists about the ecological impacts of feral horses, the size of feral herds, and appropriate methods of population control (Symanski 1996). At a practical level, the removal of animals by culling would probably be the simplest way of achieving population reduction, but public resistance precludes this option.

The infusion of strong public sentiment into policy for feral horses, as well as burros in the United States, would likely serve as a mild preview of public reaction to serious efforts to control feral cats. Ample evidence demonstrates that feral cats are the most serious threat to the persistence of many small vertebrates. Churcher and Lawton (1989) estimate that domestic cats kill annually at least 20 million birds in Britain; although the toll taken by feral cats is widely disputed, this mortality can only exacerbate the total effect of this nonindigenous species. The degree to which feral cats in Australia should be eradicated and domestic cats sterilized has already engendered vituperative debate. Similar discussion, pitting environmentalists against the general public, is being played out in the United States (Roberto 1995) and Europe. Few biotic invasions in coming decades will deserve more even-handed comment from ecologists than the dilemma of feral cats.

Game and fish agencies have traditionally been major importers of nonindigenous species, particularly fishes (Courtenay 1997), game birds (Bump 1968), and mammals (Cox et al. 1997). In Florida, for example, the Florida Game and Fresh Water Fish Commission maintains a laboratory to seek out and test nonindigenous fish species that might become attractive sport fish in the state's waters. The agency has imported several species, including the peacock bass (*Cichla ocellaris*), which is spreading, although its impacts on native species are uncertain (Courtenay 1997). Although at least some game and fish agencies have recently recognized the need for more regulation of nonindigenous species (Cox et al. 1997), the fact that they are still mandated

to import new species suggests a conflicted attitude. Furthermore, many private individuals and organizations release game species in new locations. Some releases of game fishes and other animals constitute deliberate flouting of laws. Groups of private individuals in the northern Rocky Mountains surreptitiously released nonindigenous fish into isolated mountain lakes, backpacking the fish to ensure that even the most isolated alpine lakes received what these individuals deemed as suitable biota (Ring 1995). Even apparently innocuous actions can have ecologically catastrophic impacts. The release of bait fishes by fishermen at the end of the day has already led to the extinction of species in the United States, including the Pecos pupfish (*Cyprinodon pecosensis*), through hybridization (Echelle and Connor 1989).

Long-term strategies for control of biotic invaders

Effective prevention and control of biotic invasions require a long-term, large-scale strategy rather than a tactical approach focused on battling individual invaders (Moody and Mack 1988, Anonymous 1997b, Simberloff et al. 1997). An underlying philosophy of such a strategy should be to establish why nonindigenous species are flourishing in a region and to address the underlying causes rather than simply destroying the currently most oppressive invaders. System management, rather than species management, ought to be the focus.

One of the problems of taking a tactical view of invaders, especially in a region where multiple invasive organisms are flourishing, is the prospect of simply "trading one pest for another." For example, introduction of a successful biocontrol agent against only one species may be ecologically useless unless there is a strategy in place for dealing with the remaining invaders. This unintended outcome may have already occurred, possibly in the ascendance of yellow starthistle (*Hypericum perforatum*) as a weed in California as the impact of biocontrol on St. John's wort increased in the 1950s (Mack, *in press*), and it may occur often. A strategic, system-wide approach is particularly appropriate for conservation areas, although it is seldom undertaken (Luken and Thieret 1997, Storrs et al. 1999).

In some nations, a broader strategic approach to the control of invaders is being put into place. Australia has recently adopted a national weed strategy aimed at reducing the impact of plant invaders (Anonymous 1997a). Similarly, in a project of extraordinary scale, South Africa is determined to clear all the invasive woody species from its river catchments in a 20-year program. The multispecies, multipronged strategy involves manual clearing of thickets to allow native vegetation to reestablish, treatment of cut stumps with mycoherbicides, and the use of biological control to prevent reinvasion by exotic pines. Although this program

will cost US \$150 million, it is far cheaper than alternatives such as massive dam-building programs to insure the nation's water supply, and it has the bonus of creating thousands of jobs (Anonymous 1997b).

FUTURE RESEARCH AND POLICY PRIORITIES

Extensive research on the ecology of biotic invasions dates back only a few decades (Elton 1958, Salisbury 1961). Although much has been learned, too many of the data remain anecdotal, and the field still lacks definitive synthesis, generalization, and prediction. The following include a few arenas in which research or new policy initiatives, or both, seem particularly worthwhile.

1) Clearly, we need a much better understanding of the epidemiology of invasions. As part of this goal we need much better areal assessments of on-going invasions, for both public policy decisions as well as science. Few tools are as effective as time-series maps in showing the public the course of an unfolding invasion. For example, Elton's (1958) portrayal of the geographic scale of biotic invasions gained much visual impact through his use of time-series maps. We also emphasize here the need to collect in a more deliberate manner information about the population biology of immigrations that fail (Harper 1982), since an understanding of the failure of the vast majority of immigrants can eventually help us discern the early harbingers of an impending invasion.

2) Experimentation in the epidemiology of invasions is a logical extension of 1). So far, the most comprehensive data come from observing the fates of insects released in biological control (Simberloff 1989) and birds introduced on islands (Veltman et al. 1996). We need to develop innocuous experimental releases of organisms that can be manipulated to explore the enormous range of chance events to which all immigrant populations may be subjected (e.g., Crawley et al. 1993).

3) Worthwhile economic estimates of the true cost of biotic invasions are rare and almost always involve single species in small areas. We need comprehensive cost-benefit analyses that accurately and effectively highlight the damage inflicted on the world economy by biotic invasions. The need is similar to the mandate the World Health Organization meets by analyzing and reporting the economic toll of human disease (e.g., WHO 1993).

4) Most members of society become aware of biotic invasions only through some firsthand experience, which usually involves some type of economic cost. These cases often prompt action, or at least public reaction, that is short-lived and local. We need instead a greater public and governmental awareness of the chronic and global effects of invasive organisms and the tools available to curb their spread and restrict their ecological and economic impacts. Public outreach

about biotic invaders must match or exceed current efforts that draw public attention to other ongoing threats to global change (Bright 1998, Kaiser 1999).

CONCLUSIONS

Biotic invasions are altering the world's natural communities and their ecological character at an unprecedented rate. If we fail to implement effective strategies to curb the most damaging impacts of invaders, we risk impoverishing and homogenizing the very ecosystems on which we rely to sustain our agriculture, forestry, fisheries, and other resources and to supply us with irreplaceable natural services. Given the current scale of invasions and our lack of effective policies to prevent or control them, biotic invasions have joined the ranks of atmospheric and land-use change as major agents of human-driven global change.

ACKNOWLEDGMENTS

We thank David Tilman for his foresight in organizing the Issues in Ecology series and the Pew Foundation for their financial support of the project that produced this report. We also thank Yvonne Baskin; her editing skills both improved this technical report and produced a lucid version of this report for the general audience. We are grateful to G. H. Orians for his comments on an earlier draft of the manuscript.

LITERATURE CITED

- Anonymous. 1994. Agreement on the application of sanitary and phytosanitary measures. Annex 1. World Trade Organization, Geneva, Switzerland.
- Anonymous. 1997a. Australian national weed strategy. Agriculture, Forestry and Fisheries Australia. Canberra, ACT, Australia.
- Anonymous. 1997b. The Working for Water Programme. 1996–97 Annual Report. Department of Water Affairs and Forestry. Pretoria, South Africa.
- Baker, H. G. 1974. The evolution of weeds. *Annual Review of Ecology and Systematics* **5**:1–25.
- Baker, H. G. 1986. Patterns of plant invasion in North America. Pages 44–57 in H. A. Mooney and J. A. Drake, editors. *Ecology of biological invasions of North America and Hawaii*. Wiley, New York, New York, USA.
- Barrett, S. C. H. 1989. Waterweed invasions. *Scientific American* **260**:90–97.
- Beggs, J. R., and P. R. Wilson. 1991. The kaka *Nestor meridionalis*, a New Zealand parrot endangered by introduced wasps and mammals. *Biological Conservation* **56**:23–38.
- Bensted-Smith, R. 1998. The war against aliens in Galapagos. *World Conservation* **4**:40–41.
- Bertness, M. D. 1984. Habitat and community modification by an introduced herbivorous snail. *Ecology* **65**:370–381.
- Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. *Journal of Vegetation Science* **7**:121–124.
- Bodde, M. J., A. P. Ferriter, and D. D. Thayer. 1994. The biology, distribution, and ecological consequences of *Melaleuca quinquenervia* in the Everglades. Pages 341–355 in S. Davis and J. Ogden, editors. *Everglades: the ecosystem and its restoration*. St. Lucie, Delray Beach, Florida, USA.
- Booth, R. G., A. E. Cross, S. V. Fowler, and R. H. Shaw. 1995. The biology and taxonomy of *Hyperaspis pantherina* (Coleoptera: Coccinellidae) and the classical biological control of its prey *Orthezia insignis* (Homoptera: Ortheziidae). *Bulletin of Entomological Research* **85**:307–314.
- Boppré, M., A. Biller, O. W. Fischer, and T. Hartmann. 1992. The non-nutritional relationship of *Zonocerus* (Orthoptera) to *Chromolaena* (Asteraceae). Pages 89–90 in J. H. Visser and P. Harrewijn, editors. *Insect-plant relationships*. Kluwer, Dordrecht, Netherlands.
- Braithwaite, R. W., W. M. Lonsdale, and J. A. Estbergs. 1989. Alien vegetation and native biota in tropical Australia: the spread and impact of *Mimosa pigra*. *Biological Conservation* **48**:189–210.
- Braun, E. L. 1950. *Deciduous forests of eastern North America*. Hafner, New York, New York, USA.
- Bright, C. 1998. *Life out of bounds*. Norton, New York, New York, USA.
- Brody, J. E. 1975. Agriculture department to abandon campaign against the fire ant. *New York Times*, April 20, p. 46.
- Brown, J. H. 1989. Patterns, modes and extents of invasions by vertebrates. Pages 85–109 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. *Biological invasions: a global perspective*. Wiley, Chichester, UK.
- Bullington, S. W. 1997. Regulating herps. *Vivarium* **8**(5):9.
- Bump, G. 1968. *Foreign game investigations: a federal-state cooperative program*. U.S. Department of the Interior, Washington, D.C., USA.
- Carey, J. R. 1992. The medfly in California. Response to letters to the editor. *Science* **255**:514–516.
- Carlton, J. T., and J. B. Geller. 1993. Ecological roulette: biological invasions and the global transport of nonindigenous marine organisms. *Science* **261**:78–82.
- Caster, J. 1994. Invasive alien plants on D. O. T. right-of-way managed lands. Pages 197–205 in D. C. Schmitz and T. C. Brown, editors. *An assessment of invasive nonindigenous species in Florida's public lands*. Florida Department of Environmental Protection, Tallahassee, Florida, USA.
- Center, T. D., J. H. Frank, and F. A. Dray. 1997. Biological control. Pages 245–263 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island, Washington, D.C., USA.
- Churcher, P. B., and L. H. Lawton. 1989. Beware of well-fed felines. *Natural History* **98**:40–47.
- Civeyrel, L., and D. Simberloff. 1996. A tale of two snails: is the cure worse than the disease? *Biodiversity and Conservation* **5**:1231–1252.
- Clark, J. M., D. D. Heath, and M. Stankiewicz. 1997. The ectoparasites of brushtail possum *Trichosurus vulpecula* in New Zealand. *New Zealand Journal of Zoology* **24**:199–204.
- Clout, M. N. 1999. Biodiversity conservation and the management of invasive animals in New Zealand. Pages 349–359 in O. T. Sandlund, P. J. Schei, and A. Viken, editors. *Invasive species and biodiversity management*. Kluwer, London, UK.
- Colman, P. H. 1978. An invading giant. *Wildlife in Australia* **15**(2):46–47.
- Corlett, R. T. 1992. The ecological transformation of Singapore, 1819–1990. *Journal of Biogeography* **19**:411–420.
- Courtenay, W. R. 1997. Nonindigenous fishes. Pages 109–122 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island, Washington, D.C., USA.
- Cousens, R., and M. Mortimer. 1995. *Dynamics of weed populations*. Cambridge University Press, Cambridge, UK.
- Cox, J. A., T. G. Quinn, and H. H. Boyter. 1997. Management by Florida's Game and Fresh Water Fish Commission. Pages 297–316 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island, Washington, D.C., USA.
- Crawley, M. J. 1987. What makes a community invisable? Pages 429–453 in A. J. Gray, M. J. Crawley, and P. J.

- Edwards, editors. Colonization, succession and stability. Blackwell Scientific, Oxford, UK.
- Crawley, M. J. 1989. Chance and timing in biological invasions. Pages 407–423 in J. Drake, F. di Castri, R. Groves, F. Kruger, H. A. Mooney, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Wiley, New York, New York, USA.
- Crawley, M. J., R. S. Hails, M. Rees, D. Kohn, and J. Buxton. 1993. Ecology of transgenic oilseed rape in natural habitats. *Nature* **363**:620–623.
- Crawley, M. J., P. H. Harvey, and A. Purvis. 1996. Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society of London*, **B 351**:1251–1259.
- Cronk, Q. C. B., and J. L. Fuller. 1995. Plant invaders. Chapman and Hall, London, UK.
- Crooks, J., and M. E. Soule. 1996. Lag times in population explosions of invasive species: causes and implications. Pages 39–46 in O. T. Sandlund, P. J. Schei, and A. Viken, editors. Proceedings, Norway/UN Conference on Alien Species. Directorate for Nature Management and Norwegian Institute for Nature Research, Trondheim, Norway.
- Crosby, A. W. 1972. The Columbian exchange; biological and cultural consequences of 1492. Greenwood, Westport, Connecticut, USA.
- D'Antonio, C. M., and B. E. Mahall. 1991. Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany* **78**:885–894.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics* **23**:63–87.
- Dahlsten, D. L. 1986. Control of invaders. Pages 275–302 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.
- Daubenmire, R. 1978. Plant geography. Academic Press, New York, New York, USA.
- Davidson, N. A., and N. D. Stone. 1989. Imported fire ants. Pages 196–217 in D. A. Dahlsten and R. Garcia, editors. Eradication of exotic pests. Yale University Press, New Haven, Connecticut, USA.
- Davis, C. J., and G. D. Butler. 1964. Introduced enemies of the giant African snail, *Achatina fulica* Bowdich. Proceedings of the Hawaiian Entomological Society **18**:377–389.
- De Bach, P., and D. Rosen. 1991. Biological control by natural enemies. Second edition. Cambridge University Press, Cambridge, UK.
- di Castri, F. 1989. History of biological invasions with emphasis on the Old World. Pages 1–30 in J. Drake, F. di Castri, R. Groves, F. Kruger, H. A. Mooney, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Wiley, New York, New York, USA.
- Dickman, C. 1996. Overview of the impacts of feral cats on Australian native fauna. Australian Nature Conservation Agency, Canberra, ACT, Australia.
- Echelle, A. A., and P. J. Connor. 1989. Rapid, geographically extensive genetic introgression after secondary contact between two pupfish species (Cyprinodon, Cyprinodontidae). *Evolution* **43**:717–727.
- Ehrlich, P. R. 1986. Which animal will invade? Pages 70–95 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.
- Eiten, G., and R. Goodland. 1979. Ecology and management of semi-arid ecosystems in Brazil. Pages 277–300 in B. H. Walker, editor. Management of semi-arid ecosystems. Elsevier, Amsterdam, The Netherlands.
- Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.
- Fayle, C. E. 1933. A short history of the world's shipping industry. Allen and Unwin, London, UK.
- Fearnside, P. M. 1993. Deforestation in Brazilian Amazonia: the effect of population and land tenure. *Ambio* **22**:537–545.
- Federal Register. 1997. Rules and Regulations. Department of the Interior, Fish and Wildlife Service, 50 CFR part 17, RIN 1018-AD14. Endangered and threatened wildlife and plants; determination of endangered status for two tidal marsh plants—*Cirsium hydrophyllum* var. *hydrophilum* (Suisun thistle) and *Cordylanthus mollis* spp. *mollis* (Soft bird's beak) from the San Francisco Bay area of California. Office of the Federal Register, National Archives and Records Administration, Washington, D.C. **62** (224, Thursday November 20): 61916–61923.
- Fridriksson, S., and B. Magnusson. 1992. Development of the ecosystem on Surtsey with references to Anak Krakatau. *GeoJournal* **28**:287–291.
- Goldschmidt, T. 1996. Darwin's dreampond. Drama in Lake Victoria. Massachusetts Institute of Technology Press, Cambridge, Massachusetts, USA.
- Gosling, M. 1989. Extinction to order. *New Scientist* **121**:44–49.
- Gray, A. 1879. The pertinacity and predominance of weeds. *American Journal of Science and Arts* **18**:161–167.
- Gray, A. J., and P. E. M. Benham, editors. 1990. *Spartina anglica*—a research review. ITE research publication no. 2. Natural Environment Research Council, Institute of Terrestrial Ecology, London, UK.
- Greathead, D. J. 1968. Biological control of *Lantana*—a review and discussion of recent developments in East Africa. *PANS* **14**:167–175.
- Groombridge, B., editor. 1992. Global biodiversity. Status of the Earth's living resources. Chapman and Hall, London, UK.
- Hajek, A. E., R. A. Humber, and J. S. Elkinton. 1995. Mysterious origins of *Entomophaga maimaiga* in North America. *American Entomologist* **41**:31–42.
- Harper, J. L. 1965. Establishment, aggression and cohabitation. Pages 243–265 in H. G. Baker and G. L. Stebbins, editor. The genetics of colonizing species. Academic, New York, New York, USA.
- Harper, J. L. 1982. After description. Pages 11–25 in E. I. Newman, editor. The plant community as a working mechanism. British Ecological Society Special Publications, No. 1. Blackwell Scientific, Oxford, UK.
- Heywood, V. H. 1989. Patterns, extents and modes of invasions by terrestrial plants. Pages 31–60 in J. A. Drake, F. di Castri, R. H. Groves, F. J. Kruger, H. A. Mooney, M. Rejmanek, and M. Williams, editors. Biological invasions: a global perspective. Wiley, New York, New York, USA.
- Hill, D. S., and J. M. Waller. 1982. Pests and diseases of tropical crops, Volume I: principles and methods of control. Longman, Essex, UK.
- Hoelmer, K. A., and J. K. Grace. 1989. Citrus blackfly. Pages 147–165 in D. A. Dahlsten and R. Garcia, editors. Eradication of exotic pests. Yale University Press, New Haven, Connecticut, USA.
- Holm, L., J. Doll, E. Holm, J. Pancho, and J. Herberger. 1997. World weeds: natural histories and distribution. Wiley, New York, New York, USA.
- Howarth, F. G. 1991. Environmental impacts of classical biological control. *Annual Review of Entomology* **36**:485–509.
- Huelma, C. C., K. Moody, and T. W. Mew. 1996. Weed seeds in rice seed shipments: a case study. *International Journal of Pest Management* **42**:147–150.
- Jenkins, P. 1996. Free trade and exotic species introductions. Pages 145–147 in O. T. Sandlund, P. J. Schei, and A. Viken,

- editors. Proceedings, Norway/UN Conference on Alien Species. Directorate for Nature Management and Norwegian Institute for Nature Research, Trondheim, Norway.
- Kaiser, J. 1999. Stemming the tide of invading species. *Science* **285**:1836–1841.
- Kaufmann, J. B., D. L. Cummings, and D. E. Ward. 1998. Fire in the Brazilian Amazon: 2. biomass, nutrient pools, and losses in cattle pastures. *Oecologia* **113**:415–427.
- Kaufmann, J. B., D. L. Cummings, D. E. Ward, and R. Babbitt. 1995. Fire in the Brazilian Amazon: 1. biomass, nutrient pools, and losses in slashed primary forests. *Oecologia* **104**:397–408.
- King, W. B. 1985. Island birds: will the future repeat the past? Pages 3–15 in P. J. Moors, editor. Conservation of island birds. International Council for Bird Preservation. Cambridge University Press, Cambridge, UK.
- Kruger, F. J., D. M. Richardson, and B. W. van Wilgen. 1986. Processes of invasion by alien plants. Pages 145–155 in I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. The ecology and management of biological invasions in southern Africa. Oxford University Press, Cape Town, South Africa.
- Lawton, J. H. 1987. Are there assembly rules for successional communities? Pages 225–244 in A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, succession and stability. Symposium of the British Ecological Society, volume 26. Blackwell, Oxford, UK.
- Lever, C. 1979. They dined on eland. Quiller, London, UK.
- Long, J. L. 1981. Introduced birds of the world. David and Abbott, Newton, UK.
- Lonsdale, W. M. 1994. Inviting trouble: introduced pasture species in Northern Australia. *Australian Journal of Ecology* **19**:345–354.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522–1536.
- Louda, S. M., D. Kendall, J. Connor, and D. Simberloff. 1997. Ecological effects of an insect introduced for the biological control of weeds. *Science* **277**:1088–1090.
- Lousley, J. E. 1953. The recent influx of aliens into the British flora. Pages 140–159 in J. E. Lousley, editor. The changing flora of Britain. Botanical Society of the British Isles. Arbroath, London, UK.
- Luken, J. O., and J. W. Thieret, editors. 1997. Assessment and management of plant invasions. Springer-Verlag, New York, New York, USA.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* **7**:145–165.
- Mack, R. N. 1985. Invading plants: their potential contribution to population biology. Pages 127–142 in J. White, editor. Studies on plant demography: John L. Harper festschrift. Academic Press, London, UK.
- Mack, R. N. 1989. Temperate grasslands vulnerable to plant invasion: characteristics and consequences. Pages 155–179 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Wiley, Chichester, UK.
- Mack, R. N. 1995. Understanding the processes of weed invasions: the influence of environmental stochasticity. Pages 65–74 in C. Stirton, editor. Weeds in a changing world. British Crop Protection Council, Symposium Proceedings No. 64, Brighton, UK.
- Mack, R. N. 1996. Plant invasions: early and continuing expressions of global change. Pages 205–216 in B. Huntley, W. Cramer, A. V. Morgan, H. C. Prentice, and J. R. M. Allen, editors. Past and future rapid environmental changes: the spatial and evolutionary responses of terrestrial biota. Springer-Verlag, Berlin, Germany.
- Mack, R. N. *In press*. Assessing the extent, status and dynamics of plant invasions: current and emerging approaches. In H. A. Mooney and R. J. Hobbs, editors. The impact of global change on invasive species. Island, Covelo, California, USA.
- McArthur, E. D., A. C. Blauer, and R. Stevens. 1990. Forage *Kochia* competition with cheatgrass in central Utah. Pages 56–65 in Proceedings—Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. U.S. Forest Service General Technical Report INT-276.
- McDowall, R. M. 1994. Gamekeepers for the nation: the story of New Zealand's acclimatisation societies 1861–1990. Canterbury University Press, Christchurch, New Zealand.
- McNeill, W. H. 1976. Plagues and peoples. Anchor, New York, New York, USA.
- Meinesz, A. 1999. Killer algae. University of Chicago Press, Chicago, Illinois, USA.
- Merrill, L. D. 1989. Citrus canker. Pages 184–195 in D. L. Dahlsten and R. Garcia, editors. Eradication of exotic pests. Yale University Press, New Haven, Connecticut, USA.
- Messenger, P., and R. van den Bosch. 1971. The adaptability of introduced biological control agents. Pages 68–92 in C. B. Huffaker, editor. Biological control. Plenum, New York, New York, USA.
- Moody, M., and R. N. Mack. 1988. Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology* **25**:1009–1021.
- Moran, C., and H. G. Zimmerman. 1991. Biological control of jointed cactus, *Opuntia aurantiaca* (Cactaceae), in South Africa. *Agriculture, Ecosystems and Environment* **37**:5–27.
- Mountainspring, S., and J. M. Scott. 1985. Interspecific competition among Hawaiian forest birds. *Ecological Monographs* **55**:219–239.
- Moyle, P. B. 1986. Fish introductions into North America: patterns and ecological impact. Pages 27–43 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Wiley, New York, New York, USA.
- National Research Council. 1986. Pesticide resistance, strategies and tactics for management. Committee on Strategies for the Management of Pesticide Resistant Pest Populations, Board on Agriculture. National Academy Press, Washington, D.C., USA.
- Naylor, R. 1996. Invasions in agriculture: assessing the cost of the Golden Apple Snail in Asia. *Ambio* **25**:443–448.
- Nelson, T. C. 1955. Chestnut replacement in the Southern Highlands. *Ecology* **36**:352–353.
- New Zealand Department of Conservation. 1995. Kaimanawa wild horses plan. Department of Conservation, Wanganui Conservancy, Wanganui, New Zealand.
- Odour, G. 1996. Biological pest control and invasives. Pages 116–122 in O. T. Sandlund, P. J. Schei, and A. Viken, editors. Proceedings of the Norway/UN Conference on Alien Species. Directorate for Nature Management and Norwegian Institute for Nature Research, Trondheim, Norway.
- Osmund, C. B., and L. Monro. 1981. Prickly pear. Pages 194–222 in D. J. and S. G. M. Carr, editors. Plants and man in Australia. Academic Press, Sydney, Australia.
- Ospina, P. 1998. Eradication and quarantine: two ways to save the islands. *World Conservation* **4**:44.
- Panetta, D., P. Pheloung, W. M. Lonsdale, S. Jacobs, M. Mulvaney, and W. Wright. 1994. Screening plants for weediness: a procedure for assessing species proposed for importation to Australia. A report commissioned by the Australian Weeds Committee. Canberra, Australia.
- Pannell, D. J. 1999. Paying for weeds: economics and policies for weeds in extensive land systems. Pages 571–576 in D. Eldridge and D. Freudenberger, editors. Proceedings

- of the VI International Rangeland Congress. Volume 2. Townsville, Australia.
- Perrins, J., M. Williamson, and A. H. Fitter. 1992. Do annual weeds have predictable characters? *Acta Oecologica* **13**: 517–533.
- Pheloung, P. 1995. Determining the weed potential of new plant introductions to Australia. Agriculture Protection Board Report. Perth, Western Australia.
- Pheloung, P. 1999. Preventing the introduction of potential new weeds to Australia. *Plant Protection Quarterly* **14**(3): 96–99.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience*. **50**:53–65.
- Porter, S. D., and D. A. Savignano. 1990. Invasion of polygene fire ants decimates native ants and disrupts arthropod community. *Ecology* **71**:2095–2106.
- Randall, J. M., R. R. Lewis, and D. B. Jensen. 1997. Ecological restoration. Pages 205–219 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island, Washington, D.C., USA.
- Read, D. J., D. H. Lewis, A. H. Fitter, and I. J. Alexander, editors. 1992. *Mycorrhizas in ecosystems*. CAB International, Wallingford, Oxon, UK.
- Reichard, S., and W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology* **11**:193–203.
- Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* **77**:1655–1660.
- Rhymer, J., and D. Simberloff. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* **27**:83–109.
- Richardson, D. M., I. A. W. Macdonald, P. M. Holmes, and R. M. Cowling. 1992. Plant and animal invasions. Pages 271–308 in R. M. Cowling, editor. *The ecology of the fynbos: nutrients, fire and diversity*. Oxford University Press, Oxford, UK.
- Ridley, H. N. 1930. *The dispersal of plants throughout the world*. L. Reeve, Ashford, Kent, UK.
- Ring, R. 1995. The West's fisheries spin out of control. *High Country News* **27**(17):1–6.
- Roane, M. K., G. J. Griffin, and J. R. Elkins. 1986. Chestnut blight, and other *Endothia* diseases, and the genus *Endothia*. American Phytopathological Society, St. Paul, Minnesota, USA.
- Roberto, P. 1995. The cat rescue movement vs. wildlife defenders. *California Coast and Ocean* **11**(2):31–40.
- Rodda, G. H., T. H. Fritts, and P. J. Conry. 1992. Origin and population growth of the brown tree snake, *Boiga irregularis*, on Guam. *Pacific Science* **46**:46–57.
- Roy, J. 1990. In search of the characteristics of plant invaders. Pages 335–352 in F. di Castri, A. J. Hansen, and M. Debussche, editors. *Biological invasions in Europe and the Mediterranean Basin*. Kluwer, Dordrecht, The Netherlands.
- Rozhnov, V. V. 1993. Extinction of the European mink: an ecological catastrophe or natural process? *Lutreola* **1**:10–16.
- Ruesink, J. L., I. M. Parker, M. J. Groom, and P. M. Kareiva. 1995. Reducing the risks of nonindigenous species introductions—guilty until proven innocent. *Bioscience* **45**(7): 465–477.
- Salisbury, E. 1961. *Weeds and aliens*. Collins, London, UK.
- Sandlund, O. T., P. J. Schei, and A. Viken, editors. 1996. *Proceedings of the Norway/UN Conference on alien species*. Directorate for Nature Management and Norwegian Institute for Nature Research, Trondheim, Norway.
- Savidge, J. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* **68**:660–668.
- Schardt, J. D. 1997. Maintenance control. Pages 229–243 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island, Washington, D.C., USA.
- Schmitz, D. C., D. Simberloff, R. H. Hofstetter, W. Haller, and D. Sutton. 1997. The ecological impact of nonindigenous plants. Pages 39–61 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island Press, Washington, D.C., USA.
- Semken, H. A. 1983. Holocene mammalian biogeography and climatic change in the Eastern and Central United States. Pages 182–207 in H. E. Wright, editor. *Late-Quaternary environments of the United States. Volume 2. The Holocene*. University of Minnesota Press, Minneapolis, Minnesota, USA.
- Seymour, F. C. 1969. *The flora of New England*. Tuttle, Rutland, Vermont, USA.
- Shukla, J., C. Nobre, and P. Sellers. 1990. Amazon deforestation and climatic change. *Science* **247**:1322–1325.
- Simberloff, D. 1986. Introduced insects: a biogeographic and systematic perspective. Pages 3–26 in H. A. Mooney and J. A. Drake, editors. *Ecology of biological invasions of North America and Hawaii*. Wiley, New York, New York, USA.
- Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* **19**:473–511.
- Simberloff, D. 1989. Which insect introductions succeed and which fail? Pages 61–75 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. *Biological invasions: a global perspective*. Wiley, Chichester, UK.
- Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* **49**:87–97.
- Simberloff, D. 1997. Eradication. Pages 221–228 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island, Washington, D.C., USA.
- Simberloff, D., D. C. Schmitz, and T. C. Brown. 1997. Why we should care? Pages 359–367 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. *Strangers in paradise*. Island, Washington, D.C., USA.
- Simberloff, D., and P. Stiling. 1996. How risky is biological control? *Ecology* **77**:1965–1974.
- Smith, C. S., W. M. Lonsdale, and J. Fortune. 1999. When to ignore advice: invasion predictions and decision theory. *Biological Invasions* **1**(1):89–96.
- Soulé, M. E. 1992. The social and public health implications of global warming and the onslaught of alien species. *Journal of Wilderness Medicine* **3**:118–127.
- Storrs, M. J., A. Kenyon, and W. M. Lonsdale. 1999. Strategic weed management for the aboriginal lands of the Top End. Pages 402–407 in R. C. H. Shepherd, editor. *Proceedings of the Eleventh Australian Weeds Conference*, Melbourne, Australia.
- Strong, D. R., J. H. Lawton, and R. Southwood. 1984. *Insects on plants*. Harvard University Press, Cambridge, Massachusetts, USA.
- Symanski, R. 1996. Dances with horses: lessons from the environmental fringe. *Conservation Biology* **10**(3):708–712.
- Thellung, A. 1911–1912. La flore adventice de Montpellier. *Mémoires de la Société Nationale des Sciences Naturelles et Mathématiques de Cherbourg* **38**:57–728.
- Thompson, G. M. 1922. *The naturalization of animals and plants in New Zealand*. Cambridge University Press, Cambridge, UK.
- Thompson, J. D. 1991. The biology of an invasive plant. *BioScience* **41**:393–401.
- U.S. Congress. 1993. *Harmful nonindigenous species in the United States*. Office of Technology Assessment, OTA-F-

565. U.S. Congress Government Printing Office. Washington, D.C., USA.
- van Riper, C., S. G. van Riper, M. L. Goff, and M. Laird. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs* **56**: 327–344.
- van Wilgen, B. W., R. M. Cowling, and C. J. Burgers. 1996. Valuation of ecosystem services. *Bioscience* **46**:184–189.
- Veitch, C. R., and B. D. Bell. 1990. Eradication of introduced animals from the islands of New Zealand. Pages 137–146 in D. R. Towns, C. H. Daugherty, and I. A. E. Atkinson, editors. *Ecological restoration of New Zealand Islands*. Department of Conservation, Wellington, New Zealand.
- Veltman, C. J., S. Nee, and M. J. Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. *American Naturalist* **147**:542–557.
- Vitousek, P. M. 1990. Biological invasions and ecosystem process—towards an integration of population biology and ecosystem studies. *Oikos* **57**:7–13.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* **84**:468–478.
- Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen-fixation, ecosystem effects. *Ecological Monographs* **59**: 247–265.
- Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* **238**:802–804.
- Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1990. *Manual of the flowering plants of Hawai'i*. Volumes 1 and 2. University of Hawaii Press and Bishop Museum Press, Honolulu, Hawaii, USA.
- Walker, B. H., and W. Steffen. 1997. An overview of the implications of global change for natural and managed terrestrial ecosystems. *Conservation Ecology* **2**(2):2[online: (<http://www.consecol.org/vol1/iss2/art2>)].
- Walters, H. 1979. *Vegetation of the Earth*. Second edition. Springer, New York, New York, USA.
- Wang, J.-T. 1988. The steppes and deserts of the Xizang Plateau (Tibet). *Vegetatio* **75**:135–142.
- Weiss, P. W., and S. J. Milton. 1984. *Chrysanthemonoides monilifera* and *Acacia longifolia* in Australia and South Africa. Pages 159–160 in B. Dell, editor. *Proceedings of the 4th International Conference on Mediterranean Ecosystems*. University of Western Australia, Nedlands, Western Australia.
- Welbank, P. J. 1960. Toxin production from *Agropyron repens*. Pages 158–164 in J. L. Harper, editor. *The biology of weeds; a symposium of the British Ecological Society*. Blackwell Scientific, Oxford, UK.
- Wells, M. J., R. J. Poynton, A. A. Balsinhas, K. J. Musil, H. Joffe, E. van Hoepen, and S. K. Abbott. 1986. The history of introduction of invasive alien plants to southern Africa. Pages 21–35 in I. A. W. Macdonald, F. J. Kruger, and A. A. Ferrar, editors. *The ecology and management of biological invasions in Southern Africa*. Oxford University Press, Cape Town, South Africa.
- Westbrooks, R. 1993. Exclusion and eradication of foreign weeds from the United States by USDA APHIS. Pages 225–241 in B. N. McKnight, editor. *Biological pollution*. Indiana Academy of Science, Indianapolis, Indiana, USA.
- Westbrooks, R. G. 1998. *Invasive plants: changing the landscape of America: fact book*. Federal Interagency Committee for the Management of Noxious and Exotic Weeds, Washington, D.C., USA.
- Weste, G., and G. C. Marks. 1987. The biology of *Phytophthora cinnamomi* in Australasian forests. *Annual Review of Phytopathology* **25**:207–229.
- Williams, D. F., editor. 1994. *Exotic ants. Biology, impact, and control of introduced species*. Westview Press, Boulder, Colorado, USA.
- Williamson, M. 1996. *Biological invasions*. Chapman and Hall, London, UK.
- Wodzicki, K. 1965. The status of some exotic vertebrates in the ecology of New Zealand. Pages 425–458 in H. G. Baker and G. L. Stebbins, editors. *The genetics of colonizing species*. Academic, New York, New York, USA.
- World Health Organization. 1993. *The control of schistosomiasis*. WHO Technical Report Series 830. Geneva, Switzerland.
- Zohary, D., and M. Hopf. 1993. *Domestication of plants in the Old World*. Second edition. Clarendon Press, Oxford, UK.