Issues in Ecology

Biotic Invasions: Causes, Epidemiology, Global Consequences and Control

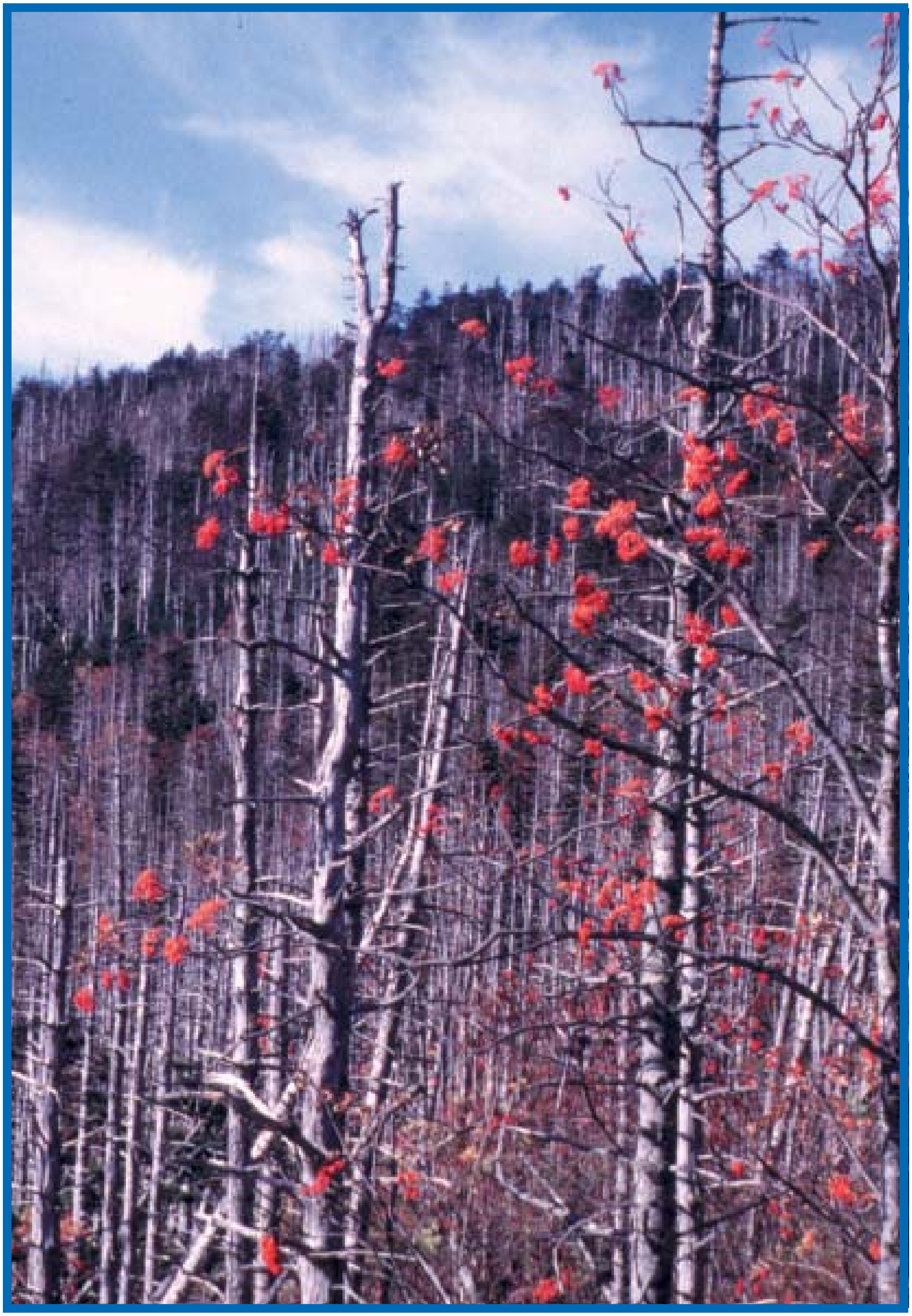

Photo by Richard Mack.

Biotic Invasions: Causes, Epidemiology, Global Consequences and Control

SUMMARY

Humans have caused an unprecedented redistribution of the earth's living things. Both incidentally and deliberately, through migration, transport, and commerce, humans are continuing to disperse an ever-increasing array of species across previously insurmountable environmental barriers such as oceans, mountain ranges, rivers, and inhospitable climate zones. Among the most far-reaching consequences of this reshuffling is a sharp increase in biotic invaders — species that establish new ranges in which they proliferate, spread, and persist to the detriment of native species and ecosystems. In a world without borders, few if any areas remain sheltered from these immigrations, and for some areas, such as oceanic islands, are subject to high rates of invasion.

Despite ubiquitous arrivals of new plants, animals and microorganisms, the fate of immigrants is decidedly mixed. Few survive and only a small fraction become naturalized. Most that do become naturalized exert no demonstrable impact in their new range. However, some naturalized species do become invasive, and these can cause severe environmental damage. There are several potential reasons why immigrants succeed: Some escape constraints such as predators or parasites, some find vacant niches to occupy, some are aided by human-caused disturbance that disrupts native communities. Whatever the cause, successful invaders can in many cases inflict enormous ecological damage.

The scientific literature reviewed by the panel makes it clear that:

- Animal invaders can cause extinctions of vulnerable native species through predation, grazing, competition, and habitat alteration.
- Plant invaders can completely alter the fire regime, nutrient cycling, hydrology, and energy budgets in a native ecosystem, greatly diminish the abundance or survival of native species, and even block navigation or enhance flooding.
- Many non-native animals and plants can hybridize with native species.
- In agriculture, the principle pests of temperate crops are non-native, and the combined expenses of pest control and crop losses constitute a "tax" on food, fiber, and forage production.
- The global cost of virulent plant and animal diseases caused by organisms 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 is a major challenge to ecology, agriculture, aquaculture, horticulture and pet trades, conservation, and international commerce. The panel finds that:

- Identifying general attributes of future invaders has proven difficult.
- Predicting susceptible locales for future invasions seems even more problematic, given the enormous differences in commerce among various regions and thus in the rate of arrival of potential invaders.
- Eradication of an established invader is rare and control efforts vary enormously in their efficacy. Successful control depends more on commitment and continuing diligence than the efficacy of specific tools themselves (trapping or spraying insecticides, releasing biological control agents).
- 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.
- Prevention of invasions is much less costly than post-entry control.

Changing national and international quarantine laws by adopting a "guilty until proven innocent" approach, instead of the current strategy of denying entry only to species already proven noxious or detrimental, would be a productive first step. The global consequences of failing to address the issue of invasions effectively would be severe, including wholesale loss of agricultural, forestry and fishery resources in some regions and disruption of the ecological processes that supply natural services on which the human enterprise depends. Given their current scale, biotic invasions have also taken their place alongside human-driven atmospheric and oceanic change as major agents of global change, and left unchecked, will influence these other forces in profound but still unpredictable ways.

Biotic Invasions: Causes, Epidemiology, Global Consequences and Control

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INTRODUCTION

Biotic invasions can occur when organisms are transported to new, often distant, ranges where their descendants proliferate, spread, and persist. 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 in the past 500 years, and especially in the past 200 years. Few habitats on earth remain free of species introduced by humans; far fewer can be considered immune from this dispersal. The species involved represent an array of taxonomic categories and geographic origins that defy any ready classification.

The adverse consequences of biotic invasions are diverse and inter-connected. 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. The aggregate effects of human-caused invasions threaten efforts to conserve biodiversity, maintain productive agricultural systems, sustain functioning natural ecosystems, and also protect human health. 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 multi-stage process that begins when organisms are transported from their native ranges to new regions. First, many, if not most, perish en route to a new locale. If they succeed in reaching a new site, immigrants are likely to be destroyed quickly by a multitude of physical or biotic agents. It is almost impossible to obtain data quantifying the number of species that are actually dispersed from their native ranges, the number that subsequently perish, and the num-

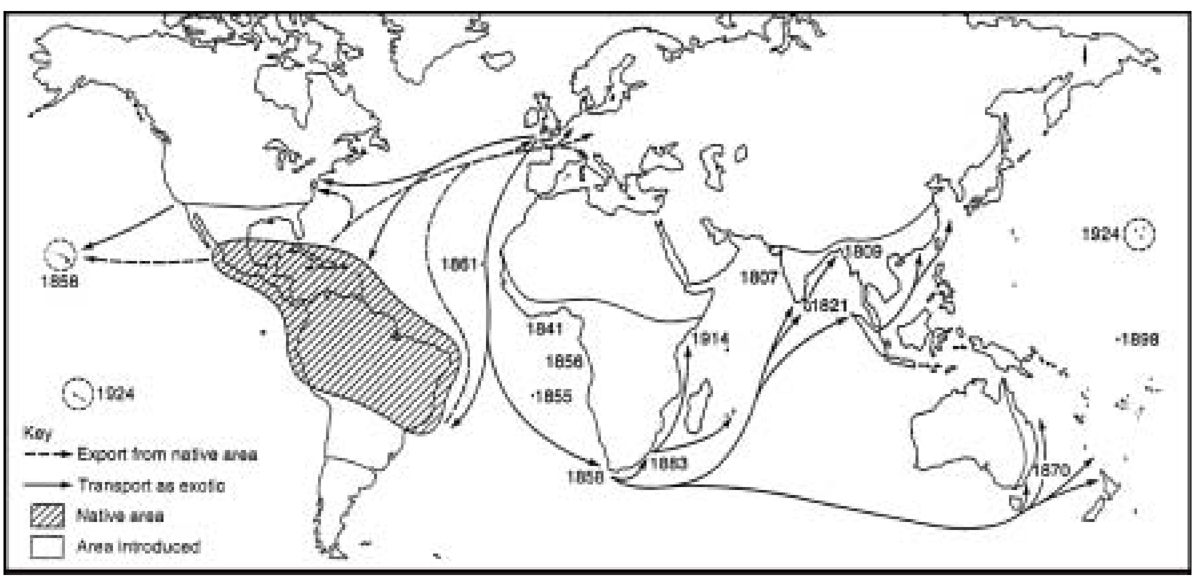

Figure 1 - Some invaders, such as the shrub *Lantana camara*, have been introduced repeatedly in new ranges, the results of global human colonization and commerce. As the array of estimated years of introduction indicates, lantana was introduced throughout the 19th and early 20th century in many new sub-tropical and tropical ranges. In each new range it has become highly destructive, both in agricultural and natural communities (Cronk and Fuller 1995).

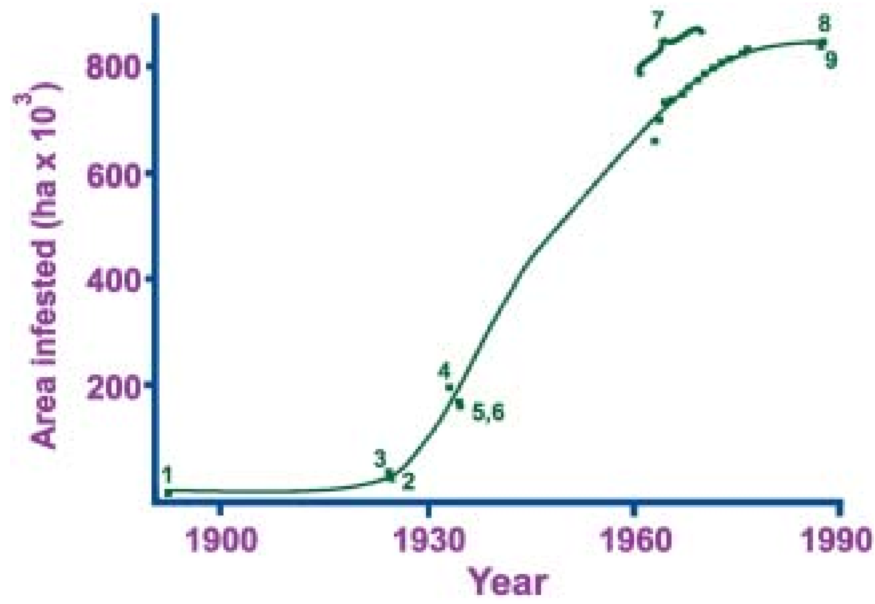

Figure 2 - Many invaders occupy new ranges at an accelerating rate with pronounced "lag" and "log" phases of proliferation and spread. This initial slow rate of range occupation may be indistinguishable from the rate of spread displayed by non-invasive (but nevertheless non-indigenous) species in a new range, thus hampering the early identification of future invaders. Terrestrial plant invasions most commonly illustrate this pattern (e.g. the spread of *Opuntia aurantiaca* in South Africa) (Moran and Zimmerman 1991 and sources [numbers 1-9] therein). By contrast, invaders in other taxonomic groups may show no lag in range expansion and rapidly occupy new range upon entry.

ber of arrivals. But, given the number of species spotted only once far beyond their native range, 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, although a greater number and frequency of new arrivals do raise the probability that a species will establish permanently.

Among the naturalized species that persist after this extremely severe reductive process, a few will go on to become invaders. An analogy is often made between epidemics caused by parasites and all other biotic invasions because many important factors in disease epidemiology have direct parallels in the study of invasions. Below we explore the epidemiology and underlying mechanisms, which 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 increase in plant, animal, and microbial immigrations worldwide roughly tracks the rise in human transport and commerce. 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. Global commerce has grown meteorically since then, providing an opportunity for a corresponding growth in biotic invasions. As a result, these biotic invasions can be viewed as predominantly post-Columbian events. Put in perspective, 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.

The proportion of various types of organisms that have invaded as a result of accidental versus deliberate movement clearly varies among taxonomic groups.

- 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 that form symbiotic relationships with the roots of most plants.
- Among insects, some deliberate introductions have had adverse consequences, including bumblebees in New Zealand. But the majority of invasive insects have probably been accidentally introduced.
- Introductions of marine invertebrates probably mirror insects. A few species have been deliberately introduced, such as the Pacific oyster imported from Japan to Washington state, but a growing number of

Photo by Richard Mack.

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Figure 3 - Invaders often alter drastically the ecosystems they occupy, over-turning native species composition, as well as changing the fire frequency, soil chemistry and hydrology. The Florida Everglades have been much altered by the collective effects of invasive plants, including *Schinus terebinthifolius* (Brazilian pepper). A) The potential natural communities across much of the Everglades are composed of small forested hammocks in a matrix of marshes. B) Invasion by Brazilian pepper has radically transformed these ecosystems into virtual monocultures of the invasive tree with devastating effects on the native biota.

invaders such as the zebra mussel have arrived as accidental contaminants in ship ballast.

- 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: rats, brown tree snakes, sea lampreys.
- Some invasive plants have been accidentally introduced as contaminants among crop seeds and other cargo. Many, if not most, plant invaders have been deliberately introduced, including some of the worst pests: water hyacinth, melaleuca trees, and tamarisk or salt cedar.

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 entails 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 (Fig. 2). This simplified scenario has many variants, of course. 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. On the other hand, many immigrant species do not become abundant and widespread for decades, during which time they may remain inconspicuous. Brazilian pepper trees were introduced to Florida in the nineteenth century but did not become widely noticeable until the early 1960's. They are now established on more than 280,000 hectares in south Florida, often in dense stands that exclude all other vegetation (Fig. 3).

During the lag phase, it can be difficult to distinguish doomed populations from future invaders. Most extinctions of immigrant populations occur during the lag phase, yet the dynamics of such a population are often indistinguishable from those of a future invader, which is growing slowly but inexorably larger. This similarity in the size and range 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. Any lag in the population growth and range expansion for a potential invader most likely results from several forces and factors operating singly or in combination:

- The number and arrangement of infestations of immigrants. Usually invasions proceed fastest among many small, widely separated infestations compared with a single larger one.

- 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.
- Natural selection that produces novel genetic types adapted to the new range. The lag phase would reflect time for emergence of newly adapted genotypes, although proof of this explanation has proven elusive.
- Habitat alteration. A lag may simply reflect the time between immigrants' entry and the later alteration of habitat (e.g. the fire regime, livestock, hydrology) that allowed their descendants to proliferate.
- 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: that is, 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.

Clearly, some immigrant populations overcome these long odds and grow to a threshold size such that extinction from chance events, demographic or environmental, becomes unlikely. One great irony about biotic invasions is that humans, through cultivation and husbandry, often enhance the likelihood that immigrants 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 human tending to persist. 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 non-native species beat the odds that defeat most immigrants in a new range.

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 concerted efforts to control them. 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. Scientifically, learning to identify invaders in advance would tell us a great deal about how life history traits evolve and how biotic communities are assembled. In practical terms, it could reveal the most effective means to prevent future invasions. 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. Evaluation of these generalizations has been difficult because they rely on post-hoc observation, correlation, and classification rather than experiments. 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. How can we know whether a community sustains 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 only by weak immigrants?

Attributes of Invaders

Biologists have long sought to explain why so few naturalized species become invaders. Intriguingly, some species have invaded several widely separated points on the planet (water hyacinth, European starlings, rats, lantana, wild oats) 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?

Many attempts have been made to construct lists of common traits shared by successful invaders. The hope behind such efforts is clear: if we can detect a broad list of traits that, for example, invading insects, aquatic vascular plants, or birds share as a group, then perhaps we can predict the identity of future invaders 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.

Relatives of invaders, particularly species in the same genera, seem to be obvious targets of suspicion as potential invaders. Many of the world's worst invasive plants belong to relatively few families and genera: Asteraceae, Poaceae, *Acacia*, *Mimosa*, *Cyperus*. Both the starling and crow families have several invasive, or at least widely naturalized, species. But most biotic invaders have few, if any, similarly aggressive relatives (water hyacinth, for instance, is the only *Eichhornia* that is invasive). This fact could simply reflect a lack of opportunities for immigration rather than a lack of talent for invasion. But the circumstantial evidence suggests otherwise: guilt by (taxonomic) association has proven imprecise at predicting invasive potential.

Community Vulnerability to Invasion

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

- Vacant niches. Some communities such as tropical oceanic islands appear to be particularly vulnerable to invasions, although the evidence can be equivocal. 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 newcomers. In contrast, however, many would-be 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 proven difficult.
- 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. 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. 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 has become an invader in New Zealand since its introduction 150 years ago. In New Zealand it has fewer competitors for food and shel-

Photo by Richard Mack.

Figure 4 - Many invasive grasses have greatly expanded their world-wide ranges at the expense of native grasslands and forests, usually facilitated by human-induced land-clearing, recurring fire, and livestock grazing. On the island of Hawaii, *Pennisetum setaceum* (fountain grass) from northern Africa has replaced the native *Metrosideros polymorpha* woodland (see remnant trees in background). It resprouts readily after its litter is burned; native plants are much less tolerant and are eventually eliminated from these sites.

ter, no native microparasites, and only 14 species of macroparasites, compared with 76 in Australia. Its population densities in New Zealand forests are tenfold greater than those prevailing in Australia. It is probably inevitable on continents that an invader will acquire new foes, especially as it expands its range and comes into contact with a wider group of native species. 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.

- Community species richness. Charles Elton proposed in 1958 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; that is, 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 multi-tiered 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. Here again, exceptions abound.
- 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. If native species can neither acclimatize nor adapt, the subsequent arrival of pre-adapted immigrants can lead swiftly to invasions. Such disturbances can be provoked by fire, floods, agricultural practices, or livestock grazing on land, or by drainage of wetlands or alterations of salinity, and nutrient 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. Alternatively, recurring natural disturbance may prevent naturalizations, such as non-indigenous species that are confined to the boundaries of a fire-prone area.

The difficulty of predicting community vulnerability to invasions is increased greatly 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. For example, for more than 300 years an ever-growing commerce has both accidentally and deliberately delivered non-native plant species to the coasts of South Africa and the Northeastern U.S. Not surprisingly, naturalized floras in these regions are very large. In contrast, some continental interiors, such as Tibet, have minuscule numbers of naturalized plants and few, if any, invaders. The native plant and animal communities 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 abundance, including extinctions of some species. These alterations constitute a threat to global biodiversity second in impact only to the direct destruction of habitat.

Biotic invaders themselves often destroy habitat, for instance by altering siltation rates in estuaries and along shorelines. In the past, the scope of this direct loss of habitat was local or at most regional. Today, however, with invasions occurring at an unprecedented pace, invaders are collectively altering global ecosystem processes. Furthermore, the growing economic toll caused by invasions is not limited by geographic or political boundaries. 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 once dominated many forests in the eastern U.S, especially in the Appalachian foothills, until the Asian chestnut blight fungus arrived in New York City on nursery stock early in the 20th century. Within a few decades, the blight had

Figure 5 - Invasive animals as well as invasive plants can radically alter both natural communities and their physical environments. *Littorina littorea* (European periwinkle) was apparently introduced near Pictou, Nova Scotia in the 1840's. Since then it has greatly increased the extent of rocky shoreline at the expense of a marsh-grass dominated zone along the New England and Canadian Atlantic coasts through its grazing on marine plants that induce siltation and mud accumulation along wave-protected shorelines.

spread throughout the eastern third of the U.S., destroying almost all American chestnuts within its native range. The mosquito 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 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 parasite.

Predation and grazing by invaders can also devastate native species. The predatory Nile perch, which was introduced into Africa's Lake Victoria, has already eliminated or gravely threatens more than 200 of the 300 to 500 species of small native cichlid fishes. 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. In Australia, cat predation takes its biggest toll on small native mammals. Cats are strongly implicated in nineteenth century extinctions of at least six species of native rodent-like Australian marsupials. Goats introduced to St. Helena Island in 1513 almost certainly extinguished more than 50 endemic plant species, although only seven were scientifically described before extinction. Invaders still extract a severe toll on St. Helena. A South American scale insect has recently threatened the survival of endemic plants, including the now rare national tree, *Commidendrum robustum*. Two years after the scale infestation began in 1993, at least 25 percent of the 2,000 remaining trees had been killed.

Non-indigenous species may also compete with natives for resources. The North American gray squirrel is replacing the native red squirrel in Britain by foraging more efficiently. The serial invasion of New Zealand's southern beech forests by two wasp species has harmed native fauna, including both invertebrates that are preyed on by wasps, and native birds which suffer competition for resources. For instance, the threatened kaka, a forest parrot, forages on honeydew produced by a native scale insect. But 95 percent of this resource is now claimed by invasive wasps during the autumn peak of wasp density, and as a result the parrots abandon the beech forests during this season. 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. They also destroy the forest cover in the highlands, thereby affecting the islands' water cycle. Invasive plants have diverse means of competing with natives. Usurping light and water are probably the most common tactics. For example, the succulent highway ice plant, *Carpobrotus edulis*, both forms a mat over native plants in coastal California and removes scarce water that the natives would otherwise use.

When a species interferes with or harms another in the competition for resources, ecologists call it interference competition, and the tactic has been well demonstrated in invasive species. For example, several widely introduced ant species — the red fire ant, the Argentine ant, and the big-headed ant — all devastate large fractions of native ant communities by aggression. Reports of interference competition among plants through their production of toxins often spark controversy, although Quackgrass, a persistent invader in agriculture, may well produce such phytotoxins.

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 threatens the existence — at least as distinct species — of both the New Zealand gray duck and the Hawaiian duck. Hybridization between a non-indigenous species and a native one can even produce a new invasive species. For instance, North American cordgrass, carried in shipping ballast to southern England, hybridized occasionally with the native cordgrass there. These hybrid individuals were sterile, but one eventually underwent a genetic change and produced a fertile, highly invasive species of cordgrass. Hybridization can threaten a native species even when the hybrids do not succeed, simply because crossbreeding reduces the number of new offspring added to the species' own population. Females of the European mink, already gravely threatened by habitat deterioration, hybridize with males of introduced North American mink. Embryos are invariably aborted, but the wastage of eggs exacerbates the decline of the native species.

Species can evolve after introduction to a new range. For example, a tropical seaweed, *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 large stretches of the seafloor, threatening nearshore marine communities. Evolution can also change potential impacts in subtler ways. A parasitic wasp imported to the U.S. to control the alfalfa weevil was originally ineffective against another insect, the Egyptian alfalfa weevil. The wasps lay their eggs in weevil larvae, providing their young with a source of food. Dissections of larval Egyptian weevils showed that 35 to 40 percent of the wasp's eggs were destroyed by the immune response of the larvae. Fifteen years later, however, only 5 percent of the eggs were being lost to these weevil defenses.

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 or melaleuca tree, which until recently was increasing its range in south Florida by more than 20 hectares per day, replaces cypress, sawgrass, and other native species. It now covers about 160,000 hectares, 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. A vine-like perennial shrub from South America, *Chromolaena odorata* or Siam weed, is not only an aggressive invader in both Asia and Africa, suppressing regeneration of primary forest trees, but also provides feeding niches that can sustain other pests. 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 (Fig. 1).

Many invasive species wreak havoc on ecosystems by fostering more frequent or intense fires, to which key native species are not adapted. The paperbark tree has this effect in Florida, as do numerous invasive grasses worldwide. In general, grasses produce a great deal of flammable standing dead material, they can dry out rapidly, and many resprout quickly after fires (Fig. 4).

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. Many other non-native plants in Hawaii are able to enter only sites with relatively fertile soils, so *Myrica* paves the way for further inva-

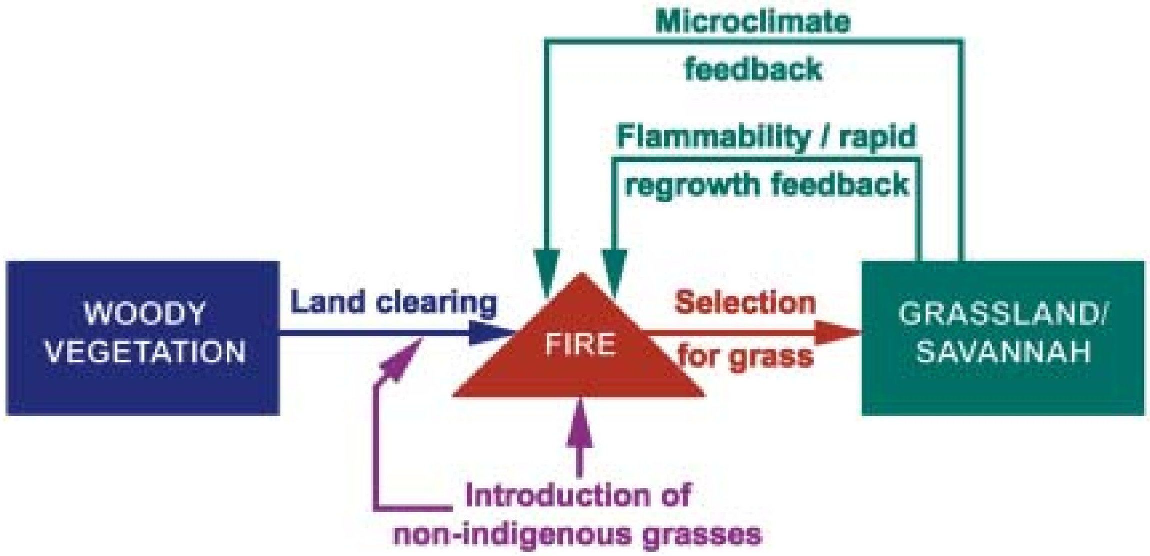

Figure 6 - Invasion of non-indigenous or alien African grasses in the Amazon Basin could eventually cause the permanent conversion of this vast forested carbon sink into grassland or savanna-like areas. Land-clearing, including wide-ranging fires, create an environment conducive to these grasses at the expense of the native species. Once these grasses occupy a site, their persistence is enhanced through their rapid annual production of highly flammable litter. This ratchet-like conversion across such a huge area holds important implications for ecosystem alteration at a global scale (after D'Antonio and Vitousek 1992).

sions, raising the threat of wholesale changes in these plant communities. *Myrica* also attracts the introduced Japanese white-eye, the most destructive invasive bird species in native Hawaiian forests and a competitor of several native bird species. The white-eye, in turn, disperses *Myrica* seeds.

Ecosystem transformations wrought by invaders have been so complete in some places 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 a Eurasian invader that supplanted the region's original vegetation, an extensive open forest and savanna with wild rye and possibly canes in the understory, after European settlement and land clearing. The European periwinkle, 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 (Fig. 5). 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 (Fig. 3) and the invasion of the fynbos or shrub communities in South Africa's Cape Province by eucalyptus, pines, acacias and other imported trees. Heavy water use by these invasive trees in South Africa has led to major water losses, and many rivers now do not flow at all or flow only infrequently. This change, in turn, has reduced agricultural production and also threatened the extinction of many endemic plant species, such as the spectacularly flowered *Proteas*.

Our best estimate is that, left unchecked, the current pace and extent of invasions will influence other agents of global change — including the alteration of greenhouse gases in the atmosphere — in an unpredictable but profound manner. The current transformation 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 livestock pastures has often involved the deliberate sowing of palatable African grasses. The spread and proliferation of these grasses has been fostered by fire. Perhaps most significant is the fact that grasslands contain much less plant biomass than the native forests and thus sequester less carbon. 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. 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 (Fig. 6).

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, forests, fisheries, and grazing capacity. Yet no other aspect of the study of biotic invasions is as poorly explored and quantified. Although 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 loss in potential economic output: that is, losses in crop production and reductions in domesticated animal and fisheries survival, fitness, and production. Second is direct cost of combating invasions, including all forms of quarantine, control, and eradication. A third category—beyond the scope of this report—would emphasize 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. One group recently attempted, for example, to tabulate the annual cost of all non-indigenous species in the U.S. They estimate that non-indigenous weeds in crops cost U.S. agriculture about $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 the group combined these types of direct losses with indirect costs for activities such as quarantine, the total cost of all non-indigenous species (plants, animals, microbes) exceeded $138 billion per year. By any standard, such costs are a formidable loss, even for a productive industrialized society such as the U.S.

These estimates illustrate the anecdotal and preliminary nature 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. When it comes to future movements of species, society needs to be able to consider results from the types of analyses 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 nonnative species into a new range; and second, concepts for curbing the spread and impact of nonnative species, including invaders, once they have established in a new range.

Preventing Entry of Nonnative Species

The use of quarantine, which is intended to prohibit organisms from entering a new range, has a long history in combating human parasites. 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, and the costs of excluding these is usually trivial compared to the cost and effort of later control after populations have grown and established. Identification of a potential future invader, however difficult, could allow marshaling of resources to bar either its entry or dispersal or to detect and destroy its founder populations soon after entry.

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). 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. The International Plant Protection Convention (IPPC) of 1951 deals with quarantine against crop pests, and the IPPC Secretariat also coordinates phytosanitary standards. The SPS agreement requires WTO members to base any SPS measures on internationally agreed guidelines.

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 World Trade Organization, in its regulatory capacity, rules that the ban is an unlawful or protectionist trade barrier rather than a legitimate attempt to exclude pests. Thus, environmental concerns and politico-economic interests may clash.

Within these international guidelines, some countries, including Australia and the U.S., have traditionally imposed quarantine controls that take an "innocent until proven guilty" approach; e.g., they have allowed entry of any non-indigenous plants that are not known to be weeds. 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.

The long-practiced U.S. approach is clearly inadequate to stem the tide of entering non-indigenous organisms, and the U. S. Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) is considering policy changes. These might involve conducting risk assessments that would estimate the invasive potential of a species proposed for import. 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 mixed success. In after-the-fact assessments of previously introduced plants, the screening system adopted by AQIS had an accuracy of about 85 percent. The current AQIS system rejects 30 percent of the species proposed for import, the vast majority "false positives" that would not have become weeds. Whether this degree of restriction on trade can be sustained remains to be seen. Such a policy risks conflict between environmentalists and commodity groups, such as horticulturists, who advocate the liberal introduction of species. Globally, society is unlikely ever to prohibit liberal movement of plants and animals in commerce. Thus, the challenge for scientists and for governments is to identify the few potentially harmful immigrants among an increasing throng of innocuous entrants.

Eradication

Eradication of a non-indigenous species is sometimes feasible, particularly if it is detected early and resources are applied quickly. Usually, however, there is insufficient ongoing monitoring, particularly in natural areas, to detect an infestation soon after it occurs. Many regulatory agencies tend however to ignore non-indigenous 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. This problem of getting agencies to take non-indigenous species seriously is exacerbated by prolonged lag times between establishment of some immigrant species and their emergence as invaders.

Nevertheless, some potentially damaging non-indigenous species have been eradicated. For example, an infestation of the Asian citrus blackfly on Key West in the Florida Keys was eradicated between 1934 and 1937. 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 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.

The giant African snail, 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 and Queensland, Australia. Local populations of non-indigenous freshwater fishes are often eradicated, and New Zealand scientists have eradicated various combinations of twelve mammal species - ranging from rodents through feral domestic animals - from many islands of up to 2000 hectares. A few non-indigenous but not yet invasive plant populations have been completely eradicated; these were all from very small areas, however.

Some eradication efforts have been successful against widespread species. For example, bacterial citrus canker was eradicated from a broad swath of the southeastern United States in the early twentieth century, and a 50-year campaign succeeded in eliminating the South American nutria from Britain. The medfly was eradicated from a substantial area of Florida in the 1930s.

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, an African root parasite of several crops in the Carolinas, has reduced the infestation from 162,000 to 6,000 hectares. 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.

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 from the southern United States has been labeled by Harvard ecologist E. O. Wilson as "the Vietnam of entomology" and was a $200 million disaster. Not only did fire ants reinvade areas cleared of ants by insecticides, but also, they returned faster than many native ant species. Further, many potential competitors and predators of fire ants were killed, and traces of the pesticides were found in a wide variety of non-target organisms, including humans. The introduced range of fire ants expanded several-fold during the 20-year campaign, and sadly, enough was known at the time about the biology of these ants that the outcome could have been predicted.

Maintenance Control

If eradication fails, the goal becomes "maintenance control" of a species at acceptable levels. 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 non-indigenous pests in agriculture. As cited above, chemical control, along with regional quarantine, has successfully contained witchweed to a few counties

Photo by Richard Mack.

Figure 7 - Mechanical control of invaders can be effective, although it usually is not practical over large areas. In some cases, however, the environmental damage outweighs the expense of labor-intensive removal. Stands of invasive trees in the Cape Province of South Africa, such as *Acacia saligna*, are so dense that their removal reveals the paucity of native plants that survived under the invader's canopy (note cleared strip at far left side of photo). Repeated detection and destruction of surviving invasive plants is essential for prolonged control.

Photo by Gary Piper.

Figure 8 - Ideally, biological control introduces a species that voraciously attacks only the target species' populations. Eventually, both target species and the biocontrol agent become rare, although usually not extinct, in the new range. The small beetle, *Chrysolina quadrigemina*, has proven to be just such an effective agent in control of invasive *Hypericum perforatum* (St. John's wort) in the U.S. and elsewhere.

in North Carolina. Chemicals remain the chief tools for battling most insect pests, and in North America such pests are almost invariably of foreign origin.

Chemical controls, unfortunately, have too often created health hazards for humans and non-target species. For example, problems associated with DDT are well known. But the frequent evolution of pest resistance, 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 from the chemicals involved, however, 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 and Florida.

Mechanical methods of controlling non-native organisms are sometimes effective and usually do not engender public criticism (Fig. 7). 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, Brazilian pepper, and other invasive plants and to plant more than 60,000 individuals of 85 native species; the volunteer time to date is valued at more than $100,000. And "hand picking" of giant African snails was a key component of the successful eradication campaigns in Florida and Queensland. However, equipment expenses, the difficulty of actually finding the target organisms, and the geographic scale of some non-indigenous species infestations frequently render mechanical control impossible.

Hunting is often cited as an effective method of maintenance control of non-indigenous animals, and hunting and trapping were crucial in many of the successful mammal eradication campaigns on small islands in New Zealand, as well as in the eradication of the nutria from Britain. In the Galapagos Islands, park officials have a long-established campaign to eradicate non-indigenous mammals, and over the past 30 years goats have been eliminated from five islands. By contrast, public hunting alone is unlikely to serve as an effective control on an invasive mammal. Public hunting of Australian brushtail possums was encouraged in New Zealand 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.

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 setting 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 in Australia by the moth *Cactoblastis cactorum* from Argentina; control of South American alligator weed in Florida and Georgia by a flea beetle; and control of the South American cassava mealybug in Africa by a South American encyrtid wasp (Fig. 8). 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 non-target species, some of them the focus of conservation efforts, have been attacked and even driven to extinction by non-native biocontrol agents. 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. 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 non-target species. For example, a Eurasian weevil, introduced to North America to control invasive musk thistle, 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. Controversy about the extent of such problems focuses primarily on two issues: whether there is sufficient monitoring to detect such non-target impacts, and the likelihood that an introduced biological control agent will evolve to attack new hosts. The fact that biological control agents can disperse and evolve, as can any other species introduced to a new range, implies that their preliminary evaluation 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 non-indigenous 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, 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 non-indigenous species. It is a large, diverse 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 introduced 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 non-indigenous species. 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. Soil Conservation Service, constituted to battle erosion, have traditionally favored non-indigenous species for these purposes. At least some state departments of transportation are moving towards use of native plants, but a long history of interaction between these departments and private horticulturists slows this process.

Figure 9 - The detrimental consequences of some invaders are only too apparent. *Eichhornia crassipes* (water hyacinth), native to the Amazon, has often been considered one of the world's worst plant invaders. In many of its new tropical ranges, it has rapidly covered the surfaces of lakes and rivers with a thick, often impenetrable, mat. Man Sagar Lake near Jaipur, India

Agricultural interests and their regulatory agencies have had a schizophrenic relationship with introduced 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 non-target 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 pet industry is also often heavily invested in non-native 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 towards threats posed by non-indigenous species and the prospect of rigorous control. However, again 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.

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, which became the target of a lengthy eradication campaign. Sometimes, pet dealers or owners deliberately release animals. 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 U.S. and New Zealand illustrate the conflicts that readily arise between environmentalists and other 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 about 500 years ago "belong" in the West, merely serving as replacements for native equids that became extinct on the continent about 10,000 years ago. In New Zealand, however, there were no native land mammals, except for bats, before introductions by people. Horses were introduced to New Zealand less than 200 years ago.

In New Zealand, feral horses have occupied the central North Island since the 1870's. Land development and hunting progressively reduced their numbers to about 174 animals in 1979. By 1981, however, public lobbying resulted in creation of a protected area for the remaining horses. With protection, horses increased to 1,576 animals by 1994, essentially doubling their population every four years. In response to damage in native ecosystems caused by this rapidly growing population, the New Zealand Department of Conservation recommended management to retain a herd of about 500 animals. 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. 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 U.S., 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. One study in Britain estimates that domestic cats alone kill 20 million birds annually; the toll for feral cats, while unknown, clearly adds to this tally. 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 U.S. and Europe. Few biotic invasions in coming decades will deserve more even-handed comment from ecologists than the dilemma caused by feral cats.

Game and fish agencies have traditionally been major importers of non-indigenous species, particularly fishes, gamebirds, and mammals. Although at least some game and fish agencies have recently recognized the need for more regulation of non-indigenous species, 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 non-indigenous 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. 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 through hybridization.

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. 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 may have already occurred — possibly in the ascendance of yellow starthistle as a plant invader in California as the impact of biocontrol on St. John's wort increased in the 1950s — and it may occur often. A strategic, system-wide approach, rather than simply destroying the currently most oppressive invaders, is particularly appropriate for conservation areas; such an approach is seldom undertaken.

In some nations, such a broader strategic approach to the control of invaders is being put into place. 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 multi-species, multi-pronged national strategy involves manual clearing of thickets to allow native vegetation to re-establish, treatment of cut stumps with mycoherbicides, and the use of biological control to prevent reinvasion by exotic woody species. 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.

FUTURE RESEARCH AND POLICY PRIORITIES

Extensive research on the ecology of biotic invasions dates back only a few decades. 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. An analogy can be made between the need for current, dynamic maps of invasions and the need met by modern weather maps. Weather maps allow viewers to recognize instantly source, direction, even intensity and collateral forces. We also emphasize here the need to collect in a more deliberate manner information about the population biology of immigrations that fail, since an understanding of the failure of the vast majority of immigrants can eventually help 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 and birds introduced on islands. 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.
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.
4. Most members of society become aware of biotic invasions only through some first-hand 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 needs to match or exceed current efforts to draw public attention to other ongoing threats to global change.

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.

Photo by Lee Foote.

Photo by Lori Randall.

Figure 10 - Nutria have caused extensive habitat damage in southern Louisiana, sometimes leading to complete loss of marsh with conversion to open water. Ariel photo shows the results of vegetative change eight months into a four year study conducted by Lori Randall and Lee Foote through the USGS National Wetlands Research Center in Lafayette, LA. Experimental exclosures protected marsh vegetation from a 80-90% reduction in standing biomass from nutria (dotted white perimeter demarcates unfenced control area grazed by nutria). Such loss of plant biomass leads to a reduction in sediment accumulation and the eventual loss of marsh habitat.

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This report summarizes the findings of our panel. Our full report, which is being published in the journal *Ecological Applications* (Volume 10, Number 3, June 2000) discusses and cites extensive references to the primary scientific literature on this subject. From that list we have chosen those below as illustrative of the scientific publications and summaries upon which our report is based.

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This report presents a consensus reached by a panel of six scientists chosen to include a broad array of expertise in this area. This report underwent peer review and was approved by the Board of Editors of *Issues in Ecology*. The affiliations of the members of the panel of scientists are:

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Yvonne Baskin, a science writer, edited the report of the panel of scientists to allow it to more effectively communicate its findings with non-scientists.

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Cover photo: Extensive death of *Abies fraseri* (Fraser fir) at Clingman's Dome, Smokey Mountains National Park. Since the arrival of the lethal insect invader *Adelges piceae* (balsam woolly adelgid) in the Park less than 30 years ago, almost all of the once prominent *A. fraseri* have been destroyed. The sparse, surviving arboreal canopy consists primarily of Picea rubens (red spruce).

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