Ecosystem Services Economics

INTERNATIONAL POLICY OPTIONS TO REDUCE THE HARMFUL IMPACTS OF ALIEN INVASIVE SPECIES

Reuben Keller
Program on the Global Environment, University of Chicago

Charles Perrings
ecoSERVICES Group, School of Life Sciences, Arizona State University



January 2010

Papers in this series are not formal publications of UNEP. They are circulated to encourage thought and discussion. The use and citation of this paper should take this into account. The views expressed are those of the authors and should not be attributed to UNEP. Copies are available from the EcosystemServices Economics Unit, Division of Environmental Policy Implementation, UNEP, Nairobi, Kenya.

TABLE OF CONTENTS

SUMMARY Error! Bookmark not defined.

1 INTRODUCTION **5**

2 A FRAMEWORK FOR UNDERSTANDING AND RESPONDING TO ALIEN SPECIES **6**

When is it best to intervene to prevent invasions? **8**

Biological invasions, poverty and environmental justice **9**

3 THE INVASION PROCESS **10**

The introduction of alien species **10**

Establishment of alien species **13**

Impacts of alien invasive species **14**

Invasive alien species and ecosystem services **16**

Invasive alien species and human health **19**

Invasive alien species that directly affect humans **20**

Invasive alien species acting as vectors for human diseases **21**

Invasive alien species impacts on food security **22**

4 INTERNATIONAL POLICY OPTIONS FOR MANAGING THE RISKS POSED BY INVASIVE ALIEN SPECIES **25**

International programs for managing emerging human diseases **27**

International programs for managing vectors of introduction **29**

The World Trade Organization and Regional Trade Agreements **31**

REFERENCES **33**

SUMMARY

Alien invasive species are a negative outcome of the closer integration of the global economic system. Trade and travel increase human welfare but also lead to the introduction and establishment of alien species. These species are transported intentionally as objects of trade (e.g., exotic animals for the pet trade) and unintentionally as contaminants (e.g., plant diseases introduced on crop germplasm). As ecosystems become more connected by human activities the number of alien species continues to grow. Impacts from invasive species are likewise growing, and are now recognized as a significant global economic burden, and one of the main drivers of global environmental change. Amongst the most significant costs of invasive alien species are their effects on human health, whether as direct agents of infection, or through their effects on water supply, food security and other ecosystem services. Although coordinated international action is required to manage species invasions, existing international agreements stop short of supporting such action for most invasive species.

All nations are affected by invasive alien species. These range from fungal crop diseases that decrease food production and security, to mollusks that infest power plants and force their temporary closure, to large predatory reptiles established in natural areas after release by pet owners. Collectively, alien invasive species are estimated to cause over a trillion dollars in global annual damages. They reduce human health and welfare, as well as the provision of ecosystem services and biodiversity. All major crops suffer large yield losses from the effects of alien species, and farmers expend much time and expense to mitigate those losses. Most human diseases, including the current H1N1 swine flu pandemic, are caused by alien species that arise in one region and spread, often very rapidly via the airline network, to other nations. The environmental impacts of invasive species are widespread and as variable as the species themselves. They include, for example, the extinction of native species, the transformation of forests to grasslands, and the reduction in the quality and quantity of freshwater supplies.

Developing nations bear a disproportionately large burden from invasive species. These nations have fewer resources both for preventing the arrival of new invaders and for controlling those already established. Agricultural pests in developing countries decrease food security more severely because these nations have greater reliance on domestic food production. Alien invasive human diseases also have greater impacts in developing nations where there is less capacity for sanitation measures and disease treatment. Finally, emerging infectious diseases such as SARS are appearing more often in developing nations, partly because of close contact between humans and animals that carry and transmit zoonotic diseases.

Preventing the spread and establishment of alien invasive species is an international public good. The risk facing any nation depends both on the efforts made by its trading partners to ensure alien species are not exported, and on its own programs for preventing the arrival and spread of new species. But although the actions of each country confer benefits on other countries, they have little incentive to take these benefits into account and every incentive to free-ride on the preventive actions of others. The result is that invasive species control is everywhere undersupplied. Addressing this problem requires coordinated action to identify and control the spread, through trade and travel, of potentially harmful species. It also requires the generation and dissemination of information on invasive species risks to enable nations to more fully utilize available international treaties (e.g., the SPS agreement) to restrict trade when risks are unacceptably high. Detailed global risk profiles for alien species are already generated for organisms that cause human diseases, and some animal and plant diseases. These support the internationally coordinated actions of the World Health Organization and Centers for Disease Control. Information about the international risks of most other alien species is rarely available, however, and there are few international agreements or agencies that could support coordinated international action based on those risks.

The problem is exacerbated since invasive species control is frequently a 'weakest-link problem'. That is, the international control of harmful species is only as good as the control exercised by the least effective nation. International action should therefore have a focus on raising the capacity of the weakest links in the chain. This could be achieved in part by establishing an international and publicly available database of known invasive species, detailing their current and potential locations and how they can be transported. This would allow all nations to modify their trade practices to reduce global invasion risks. At the same time, confronting industries with the full costs of the invasive species that they transport would encourage innovative efforts to prevent invasions, and would prevent the transfer of invasive species costs to broader society.

Many benefits would flow from strengthening international policy for preventing the spread of alien invasive species. The International Health Regulations (IHR) provide a good model for addressing the global risks posed by many invasive species. Harmonization of other international policy instruments, such as the Sanitary and Phytosanitary (SPS) Agreement, with the IHR would both recognize the common processes involved in the transport of all alien species, and provide stronger mechanisms for preventing the spread of all invasive species. There is also scope to strengthen the role of regional trade agreements in containing the risks posed of spreading invasive species within the areas covered by the agreement.

KEYWORDS: Alien invasive species, trade externality, Multilateral Environmental Agreements, biodiversity change

1 INTRODUCTION

Anthropogenic Environmental Change

Humans are having unprecedented impacts on the structure and function of ecosystems across the globe. The main drivers of ecosystem change include increased greenhouse gas emissions (Flannery 2006), increased nitrogen deposition (Vitousek et al. 1997), the conversion and fragmentation of landscapes for human use (Daily et al. 2003), and the spread of alien species (Mack et al. 2000). In many cases these impacts combine synergistically so that total effects are greater than the sum of the parts. The effects of global climate change, for example, are hastening and intensifying biodiversity losses in ecosystems already stressed by species invasions and habitat loss (Thomas et al. 2004). Most anthropogenic drivers of environmental change, including climate change (Rignot 2006, IPCC 2007, Kopp et al. 2009) and species invasions are expected to increase in the future, leading to greater stresses on ecosystems.

The ecological effects of global environmental change have profound consequences for human societies. At the global scale, the supply of many ecosystem services has declined over the last fifty years as people have transformed ecosystems for the production of food, fuels and fibers (Millennium Assessment 2005, Dobson et al. 2006). The Economics of Ecosystems and Biodiversity report is currently attempting an assessment of the impact of the changes noted by the Millennium Ecosystem Assessment on human well-being, drawing on the many existing studies of the drivers of ecosystem change, of the market value of ecosystem services that are bought and sold, and the value that people place on ecosystem services that lie outside the market (Mooney et al. 2005, www.teebweb.org). While there is much yet to learn about the value of many non-marketed ecosystem services, enough is known about the impact of environmental changes on the things that people care about most directly – human health and food security – to be able to identify and evaluate the options for managing many of the main drivers of change. This working paper focuses on one set of drivers, those relating to the dispersion of species through trade, transport and travel.

Alien Species

Alien species have drastically altered patterns of biodiversity (Ricciardi et al. 1998) and the supply of all main ecosystem services (Fischer et al. 2006, Pejchar & Mooney 2009) across the globe. Many alien species impose significant costs on people. They pose direct or indirect threats to human health, to the production of foods fuels and fibers, to the provision of freshwater and to the generation of energy supplies (Pimentel 2002). They also affect both the structure and function of ecosystems. Indeed, alien species are predicted to remain one of the greatest drivers of environmental change for the foreseeable future (Sala et al. 2000).

The growth of the invasive species problem is a byproduct of globalization (Perrings et al. 2010). As human societies become more connected through trade and travel the

opportunities for species transport increase. Many pathways of introduction are intentional, including the trade in species as pets, horticultural plants and livestock. Other pathways arise unintentionally, including the transport of aquatic species in ballast tanks of intercontinental ships (Mills et al. 1993; Ricciardi 2006), the introduction of plant species as seed contaminants on various agricultural products (Sheley et al. 1999), and the accidental introduction of livestock, wildlife and plant diseases with infected organisms (Daszak et al. 2000, Ivors et al. 2006). Alien species have often been, or have carried, human diseases and parasites (Reed et al. 2004, Jones et al. 2008).

Although individual alien species have long been recognized to have negative consequences (Coates 2006), it was only in the second half of the twentieth century that ecologists began to recognize the common processes involved in invasions. Charles Elton's book The Ecology of Invasions by Animals and Plants (1958) is generally credited with launching this awareness, and in it he related globalization to the many pathways of species introduction. The linkages between globalization and invasions are now better resolved and in many cases show a strong positive correlation between trade volumes and the number of alien species introduced. For example, the rate of alien species arrival in the Laurentian Great Lakes is strongly related to volume of shipping traffic (Ricciardi 2006), and new alien species in San Francisco Bay tend to arrive from regions connected to the Bay most strongly by shipping traffic (Costello et al. 2007).

In the absence of effective defensive policies at the national level, or of international cooperation to contain invasive species risks at the international level, continued trade growth will lead to increasing numbers of alien invasive species, with increasing costs to environments, economies and human health (Levine & D'Antonio 2003). In this paper we identify the ecological and economical processes that lead to invasion, and outline the policy options for preventing the arrival and further impacts of harmful alien species. In what follows we unpack the factors behind the introduction of invasive species. We then provide a framework for understanding the impact of invasive alien species on ecosystem services generally, before concentrating more closely on the effect of invasive species on food security and production, and human health. We conclude with a discussion of national and international policy options for managing the introduction and impacts of potentially invasive alien species.

2 A FRAMEWORK FOR UNDERSTANDING AND RESPONDING TO ALIEN SPECIES

Part of the difficulty in addressing the problem of alien invasive species is that it is dealt with very differently by different disciplines. As with many other environmental problems, both the science and management of invasive species has been split between a number of different sciences and agencies. The introduction and spread of human pathogens, for example, is seen

as a problem of medicine, public health and epidemiology. Crop and livestock pests and pathogens are seen as a problem for agricultural science. Impacts on natural ecosystems and biodiversity are addressed within ecology and conservation biology. While specialization undoubtedly offers some benefits, it also imposes significant costs in terms of our ability both to understand and address the problem. In very many cases, impacts on human, animal and plant health, on agriculture, forestry and fisheries, on species richness and abundance in 'natural' ecosystems, flow from the same process – and sometimes from the same species. In all cases, species dispersal and the consequences of that are a risk arising from peoples' decisions about trade, transport and travel. In all cases, too, the ability and willingness of a nation to manage invasive species issues depends on the value at risk, and the resources available to address the problem (Perrings et al. 2002, Shogren et al. 2009).

Globalization – the process of increasing trade, travel and communication among societies – has generated many benefits for human welfare. The increasing rates of alien species transport and establishment is, however, a side effect of that process. The introduction of alien species is said to be an externality of trade, and is not taken into account by those involved in trade (Perrings et al. 2002, Perrings et al. 2005). That is, the impacts of invasive alien species are not incorporated into the costs of doing trade, meaning that those who actually transport alien species have no economic incentive to reduce the invasion risks inherent in their business. For example, the global horticultural trade is responsible for many thousands of invasions of plants and plant diseases around the world. These invasive alien species devastate many forest ecosystems, and in many cases increase the costs of producing agricultural products. The costs of these invasions have not, however, been carried by the importers and retailers who choose which plants are appropriate for introduction, how widely those species should be marketed, and how much money should be spent to ensure that the plants are not introduced with other diseases or pests (Perrings et al. 2005). Instead, the costs of invasions are usually borne widely by society as government agencies spend taxpayer dollars to address invasion issues, and as the agricultural sector passes on the higher costs of producing food.

Part of the problem is that the control of species invasions is a public good. The benefits it offers are almost always shared among those at risk of being invaded (Perrings et al. 2002). Thus, the economic motivation at the level of an individual country is often to protect its own borders, but not to spend resources preventing the export of invaders. This is a poor way to serve the international public good, because the invasion risk to which a country is exposed depends on the actions of its neighbors and trading partners. Returning to the example of plant disease introduction through the trade in ornamental plants, it can be seen that an importing country faces risks that depend both on the effort expended by the exporter to ensure that their product is free from disease, and on the programs it runs to monitor and quarantine imported plants. In turn, countries that neighbor or trade with the importer face invasion risks based on the same factors, as well as the effort expended by the importing country to control an invasive plant disease if it becomes established. For this reason, defensive policies can never be sufficient. International cooperation is necessary to assure the public good.

In the case of a highly dispersed invasive species, or one that could become so, the public good from invasion prevention is frequently a 'weakest-link' problem (Perrings et al. 2002).

That is, the rate of spread is most affected by the nations or trades that operate the least effective programs to eradicate or control the species. This is clearly illustrated in the role of the air transport industry in the transmission of human diseases (Mangili & Gendreau 2005). Once a disease, such as SARS or H1N1 swine flu, is established in a country the only way to reduce the chance of that disease spreading is to restrict air travel (but this is not an airline decision). If such precautions are not taken, or if they are ineffective, diseases can spread rapidly across the globe. It is clearly a global public good for disease spread to be arrested as early as possible during an epidemic, but the structure of the air transport system is such that the protection enjoyed by all countries is only as good as the protection offered by the least effective regulator – the weak link. The result may be widespread and rapid infections, even in countries that operate relatively effective systems.

It is important to point out that complex feedbacks exist between the arrival and ecology of an invader and its eventual impacts (Shogren et al. 2000, Finnoff et al. 2009). That is, impacts are not simply a one-way forcing of the alien species on the invaded ecosystem. Instead, the level of impact from any invasion depends on the ecology of the introduced species, and the way that humans are able to mitigate or adapt to its impacts. For example, the arrival and spread of any invasive agricultural weed will depend on the capacity of farmers to control the species manually or with herbicides, or to adjust their cropping practices to reduce losses.

When is it best to intervene to prevent invasions?

The options for managing invasive species spread should be implemented within a cost-benefit framework. If an invasion is likely to have relatively mild impacts and would be very expensive to prevent, it may be economically optimal to allow the invasion to proceed and simply adapt to the damages. In contrast, if an invasion is likely to be very damaging then it may be most cost-effective to employ extensive proactive programs to prevent its arrival and spread. In the few cases that the cost-effectiveness of managing invasions versus adapting to their impacts has been investigated, results show that the most cost effective option is generally to prevent introductions (e.g., Leung et al. 2002, Keller et al. 2008). Keller et al. (2007) investigated a whole industry – the trade in ornamental plants in Australia – and showed that restricting importation of risky species is less costly than allowing importation of all species and suffering the costs of the inevitable invasions.

One reason why prevention is generally better than cure is that for species known to pose an invasion risk, or for import categories known to harbor such species, the range of options available to reduce impacts is greatest before a species is established. Options include restricting trade in a species of concern, requiring exporting businesses to ensure that invaders do not leave their shores, or operating quarantine facilities at the point of import (Lodge et al. 2006). In contrast, established alien species can generally only be controlled through expensive techniques such as manually pulling plants, shooting animals, or the use of herbicides and pesticides. Prior to introduction there are also more opportunities to shift the burden of responsibility to the industries that profit from risky trades in live organisms (Perrings et al. 2005). For example, most plant imports to the U.S. are required to be accompanied by a phytosanitary certificate. This certifies that the plants were produced at a

growing facility that follows high standards for the control of plant diseases and parasites. The costs for obtaining certificates, and for producing relatively safe plants for export, are borne by the trades. Without this program the costs from invaders would be borne more broadly across society.

Biological Invasions, Poverty, and Environmental Justice

Environmental change and degradation tend to have greater negative impacts on poorer societies because their economies are more heavily dependent on the exploitation of natural resources. These resources are often highly vulnerable to the effects of invasive species, especially where subsistence farming is common (Perrings 2007). Although the links between poverty and invasive alien species have not been well studied (but see case studies below), Perrings (2007) gives three reasons to believe that poor nations bear an excess burden from alien species, and that this burden will grow as global trade volumes increase.

First, because the strength and scope of border efforts to intercept invasive species are likely to be positively correlated with GDP, increasing trade levels will disproportionately impact the poorest nations. That is, an increase in trade volume is more likely to lead to an invasion in a developing nation than the same increase in a wealthy nation. Second, conservation, pest control and public health efforts are also likely to be positively correlated with GDP. Again, this will lead wealthier nations to experience a lower burden from any invasive species than would occur in a poorer nation. Third, invasive species can have massive impacts on agricultural production, and livelihoods in poor nations are more tied to agriculture. These three points suggest that poorer countries are more likely to have invasive species introduced and are less likely to control invaders if they establish. This leads to greater effects on agricultural production, which are more detrimental to human welfare in poorer countries.

Another line of evidence that poorer countries will be more exposed to invasive species risks comes from the asymmetry of ballasting activities by large trans-oceanic ships. To maintain safe trim, ships that are not full of cargo compensate by taking on ballast water. This water, and any organisms taken up with it, is discharged as the ship is loaded. Poorer countries are more likely to be exporters of bulk materials (e.g., iron ore, woodchips), while wealthy countries are more likely to import and refine those materials. The ships that transport bulk materials are generally purpose built for the specific cargo, and thus travel with empty holds to the exporting nation. This leads to a net transport of ballast water, and the invasion risk associated with it, from wealthier to poorer countries (Drake and Keller 2004).

Much less in known about the economical and ecological impacts of invasive species in poorer than in wealthier countries. Poorer nations have lower capacity and funding for the scientific studies and outreach that have helped to raise awareness of invasive species issues in countries like Australia, New Zealand and the United States. For the reasons outlined above, however, it is reasonable to assume that global trade patterns, combined with the varied wealth of nations, leads to a situation where the welfare of citizens of poorer nations is more severely impacted by invasive alien species than the welfare of citizens in wealthy nations. This disparity in invasion risks caused by international trade presents a significant

challenge for international environmental justice. The weakest-link problem means that it is also a direct source of concern to high income countries, independent of any ethical concerns.

3 THE INVASION PROCESS

To properly understand and respond to alien species it is essential to understand the linked economic, ecological and social factors that lead to their introduction, establishment, spread and impacts. Human trade and travel create diverse opportunities for the transport of live organisms. Whether species are deliberately or accidentally introduced, the result is the outcome of an economic process. Once a species has been introduced, the ecology of the species, and the ecosystem it is released into, are important determinants of whether it will persist. But the decisions that lead to its presence, or that later lead to its control, are economic decisions. The value that people place on either the ecosystems or economic activities at risk determines whether an introduced species that establishes and spreads is considered 'invasive'. These steps form the 'invasion process', and are described in Box 1. In the following section we describe the introduction, establishment and impacts of alien species in more detail.

Box 1: Invasion Process and Terminology

We define an alien species as one that is found beyond its native range as a result of human activities. The first step in the invasion process is for a species to be introduced beyond its native range. A plant imported for the horticultural trade is referred to as introduced once it is imported to a new region.

If an alien species survives and begins to reproduce beyond human cultivation (i.e., escapes into the wild and breeds), it is referred to as established. This occurs when a population of a species is found to persist for multiple generations in a setting where humans are not intentionally propagating it.

Finally, if the species begins to spread and to cause harm to society, it is referred to as invasive. This occurs when a species spreads beyond its original site of introduction and comes to be perceived as a nuisance. Invasive alien species can have a range of economic, ecological and human health impacts (see text). We note that other definitions of invasive are in use. The definition just given (and used throughout this paper) is that used by the Conventional on Biological Diversity (CBD).

The Introduction of Alien Species

Humans transport a wide taxonomic range of species for many reasons and in numerous ways. We identify three principal categories by which humans move alien species. First,

many organisms are deliberately transported intentionally for economic reasons. These include plants for the horticultural trade, animals for pets, and the many species transported as crops and livestock. These species are usually a source of economic benefits. At the same time, all of the pathways by which humans intentionally transport species also lead to opportunities for the unintentional transport of alien species. The seeds of weedy plant species may be transported in the soil of horticultural plants, and live fish shipments are often contaminated with parasites, diseases, or other fish species. Third, human activities not associated with the trade in live organisms can lead to unintentional species transport. For example, organisms are regularly transported in the ballast tanks or attached to the hulls of ships, and diseases such as SARS can be spread unintentionally when infected people travel.

We refer to the different trade and travel routes and modes as 'pathways'. Hence, the pet trade between tropical and temperate countries can be seen as a pathway, as can the movement of ships between the same set of countries. It follows that any one pathway may involve multiple vectors. For example, the global trade in horticultural plants involves many different companies and many different modes of shipment. Similarly, global ship movements can vector species movements through ballast tanks, attached to hulls, or in shipping crates. In Table 1 we provide brief descriptions of a number of vectors that transport either a large number of species, or a small number of highly damaging species. This list is illustrative, not exhaustive. Indeed, because almost all human activities that cross the boundaries of species ranges transport organisms, an exhaustive list would be enormously long. Instead, Table 1 is designed to give a broad description of the types of human activities that lead to species transport. In Box 2 we describe a subset of pathways and vectors in more detail.

Box 2: Some Important Pathways and Vectors

Horticulture trade: The ornamental trade is the strongest pathway for the introduction of alien plant species (Reichard & White 2001, Dehnen-Schmutz et al. 2007). This trade rapidly transports a huge diversity of species around the world to meet the demand of gardeners for exotic species. For example, at least 25,360 alien species have been imported to Australia for the ornamental plants trade (Virtue et al. 2004), many more than the ~15,600 native plant species in that country. Plants introduced for outside planting are usually environmentally matched to the recipient region, making them more likely to successfully establish.

Ornamental Pet Trade: Human desires for exotic pets drive a massive international trade in animals as diverse as snakes, rats, fishes and spiders. These organisms are transported rapidly around the globe, usually with little attention to the potential for the species or its contaminants to be become established. At least 4,202 vertebrate animal species, representing ~14% of the global vertebrate fauna and ~75% of families, have been imported to the US through the pet trade (Romagosa et al. 2009). As well as including huge taxonomic diversity this trade includes massive numbers of individuals. Between 2000 and 2005 over 1billion individual fish were imported to the US (Smith et al. 2008), and the ornamental fish trade is growing globally at 14% per year (Padilla & Williams 2004). The volume of fish and other pet species imported is generally far in excess of the capacity of quarantine agencies, and most shipments are not checked for diseases or other hitchhiker species.

International aid programs: International aid programs often aim to increase human welfare, and this can often be achieved by providing alien species (e.g., crops, fishes for aquaculture) and the means for their production. Species introduced for aid programs have a high chance of becoming invasive because they are generally selected to grow vigorously and with little cultivation, and because they are usually promoted and distributed widely by well-funded organizations. In terms of the invasion process, this equates to high environmental match and high propagule pressure. This has been the case in Africa where tilapia fishes, especially the Nile tilapia (*Oreochromis niloticus*), have been distributed by aid programs for aquaculture. Nile tilapia frequently escape aquaculture ponds and outcompete native fishes in natural waterways, leading to loss of biodiversity and changes in the fish caught in artisanal fisheries (Weyl 2008).

Air travel: Air travel facilitates the rapid movement of humans and cargo across the globe. As flying becomes more common the opportunities for hitchhiker species to travel long distances and survive the journey increases. Most notably, this pathway has lead to the rapid spread of a number of human diseases, including HIV, SARS and more recently the H5N1 and H1N1 influenza strains. The speed of air travel means that infectious humans can travel long distances without knowing that they are carrying serious diseases. Combined with the favorable conditions in an airplane for disease transmission, this leads to higher rates of spread, and ultimately higher impacts, from a broad range of diseases (Mangili & Gendreau 2005).

Global Shipping: Ships take on and discharge ballast water to compensate for changes in the mass of cargo carried. Organisms can be taken on with ballast and transported long distances before being released into the port where ballast is discharged. This is by far the strongest vector for the transport of marine species (Carlton & Geller 1993), and has also transported many species among freshwater habitats (Ricciadi 2006). Because global shipping volumes are increasing, and because ships now effectively link all ports into a global network, the number of invaders from this pathway may increase in the future.

Canals: Human settlements are often placed on or near rivers because shipping offers a relatively cheap way to transport goods. Thus, land barriers between waterways can increase transportation costs. To overcome these limitations, canals have been constructed in many countries to facilitate commercial transport. These canals also facilitate recreational travel and are used for the delivery of water for domestic, agricultural and industrial uses. By connecting previously isolated waterways these canals allow for the movement of alien species. For example, the construction of the Rhine-Main canal has created a navigable water connection from the Black Sea in Eastern Europe, along the Danube River and through the Rhine River to the Atlantic and North Sea (bij de Vaate et al. 2002). This canal system and others around the world have allowed the spread of many invasive alien species far beyond their native ranges (e.g., Mills et al. 1993).

Table 1: A selection of transport pathways and vectors that move organisms outside their native ranges. Neither the list of pathways nor vectors is exhaustive. See text and Box 2 for more detailed descriptions of a selection of pathways and vectors.

Transport pathway	Vector
Pathways associated with intentional transport of organisms	
Trade in ornamental plants	• Intentional transport of desirable plants • Unintentional transport of plant diseases, parasites or seeds in soil
Pet trade	• Intentional transport of animals • Unintentional transport of diseases, parasites, or whole organisms
Live food	• Organisms imported for sale at live food markets • Unintentional introduction of diseases
Intentional release for hunting and/or food	• Fishes (e.g., trout) and mammals (e.g., rabbits) released to provide new opportunities for angling & hunting
International aid programs	• Intentional transport of organisms to establish new farming opportunities
Trade in livestock	• Diseases and parasites of livestock
Biological control	• Organisms intentionally released to control pest species
Pathways that lead only to the unintentional transport of organisms	
Shipping	• Organisms in ballast tanks • Insects living in wood of packing crates • Fouling organisms attached to hull
Air travel	• Organisms entrained outside planes (wheel wells, engines) • Human diseases transported by infected passengers
Canals	• Species spread through canals to reach new watersheds

Establishment of Alien Species

While the introduction of alien species is driven almost exclusively by economic factors, species establishment depends on a balance of economic and ecological factors. One of the best-known principles of invasion biology is that species are more likely to become established if many individuals are released and if multiple introductions occur over long periods of time (Veltman et al. 1997, Duncan et al. 2001, Lockwood et al. 2005, Leung et al. 2006, Moyle & Marchetti 2006, Drake & Jerde 2009). High propagule pressure allows alien species to overcome Allee effects, a syndrome of demographic factors that leads to negative growth rates in small populations. The most common causes of Allee effects are the difficulty of finding mates when population densities are low, and mortality events (e.g., disturbance such as a storm) that can drive small populations extinct (Drake & Lodge 2006). The propagule pressure required to establish a population depends on many factors, including the condition of the organisms released, the seasonal timing of their release, and basic natural history factors such as how long the species lives (e.g., can it survive long

enough to find mates). So while the volume and frequency of trade is the primary determinant of propagule pressure, the level of propagule pressure that leads to establishment depends on a number of ecological factors.

Regardless of propagule pressure, a species will not become established unless it is environmentally matched to its new environment (Peterson 2003). For example, the probability that a tropical fish species will become established in a temperate zone lake is exceedingly small. Environmental match depends on both the natural history and ecology of the species, and on the biotic and abiotic conditions of the receiving environment. Some important factors on the species side are whether it can survive the temperature and water regimes of the new environment, and whether it is adapted to exploit available food resources. Important factors on the receiving environment side are the presence of predators, competitors or diseases that could affect the introduced species, and whether the environment has recently been disturbed in a way that would open up 'ecological space'. Elton (1958) argued for a niche-based view of invasion resistance – that more species-rich ecosystems are less likely to be invaded because resources are already fully divided among the resident species. This idea is supported by experimental studies (e.g. Fargione & Tilman 2005) but observational studies tend to show the opposite effect – that ecosystems with more native species contain more established nonindigenous species (e.g. Stohlgren et al. 2003). The mechanisms behind these results are not fully known, but they show all environments to be invasible if well-matched species are introduced with high propagule pressure.

Receiving environments may be more susceptible to invasion when they are disturbed, for example by roads (Gundale et al. 2005). Disturbances remove some proportion of the resident biota, temporarily increase available resources, and in many cases create new habitats. Anthropogenic disturbances are distinctive because humans repeatedly create similar urban and agricultural habitats, and these habitats are often better matched to alien species than natives. For example, a relatively small number of species, including the starling (*Sturnus vulgaris*), pigeon (*Columba livia*) and brown rat (*Rattus norvegicus*), are well adapted to urban environments and have become widely established across the globe.

The factors described above interact in complex and dynamic ways to determine whether an introduced alien will become established. D'Antonio et al. (2001) have formalized this into a model in which the invasibility of an ecosystem varies over time (e.g., in response to weather changes, population cycles of resident species). When an ecosystem is relatively invasible fewer propagules are required to cause species establishment, and species that are less environmentally matched to the receiving environment may be able to persist. When the ecosystem is more resistant, additional propagules will be needed. Although this model is intuitively appealing, applying it quantitatively to a real ecosystem would require intense study of the ecosystem over a long period of time, and in most cases it will subsequently be impractical to use as a tool for managing the invasion process.

Impacts of Alien Invasive Species

Although invasive species are established across the globe, the probability of an introduced species passing through all steps in the invasion process is generally low. Most introduced

species fail to become established, and those that do usually persist at low densities with no described impacts (Williamson 1996). For plants, the proportion of introduced species that become invasive is generally <5%. Depending on taxa and vector, available data indicate that 10-50% of introduced animal species become invasive (Jeschke & Strayer 2005, Romagosa et al. 2009). Despite these low proportions, the total number and impacts of invasive species are large and growing because so many species are being introduced.

The impacts of invasive species can be categorized in several ways. Table 2 illustrates the direct impacts of alien invasive species on the production of foods, fuels and fibers. Table 3 illustrates their impact on ecosystems. The following section focuses on human health.

Table 2: Some economic impacts of invasive species, organized by affected sector. The table is not comprehensive, but is designed to give an idea of the range of taxa that become invasive, and the range of their economic impacts.

Impact	**Main taxonomic groups**	**Example**
Agriculture		
Herbivores consume crops	Insects, birds, mammals	Golden apple-snail (*Pomacea canaliculata*) consumes rice and reduces yields across Southeast Asia[1] (see Box 7)
Plant pathogens infect crops, reducing yields	Viruses, bacteria, fungi	Banana bunchy top virus is infesting banana plantations worldwide, reducing food production and security, especially in Africa[2]
Pathogens infect livestock	Viruses, bacteria	Foot and mouth (*Aphtae epizooticae*) disease leads to culling of sheep and cattle herds[3]
Weedy plants overgrow agricultural fields	Grasses, herbs, shrubs, trees, vines	Kudzu (*Pueraria Montana*) vine overgrows farming land in the US, causing an estimated $500million/year in lost productivity[4]
Fisheries		
Predators consume valuable fish	Fishes, crayfishes	Nile tilapia (*Lates niloticus*) introduction to Lake Victoria has decimated wild-harvest aquarium fishery[5]
Industry		
Fouling organisms infest water pipes	Mollusks, aquatic plants	Zebra mussel (*Dreissena polymorpha*) infestations in the US and Britain require power plants to temporarily shut down to clean pipes[6]

Sources: [1]Joshi 2005; [2]Kumar & Hanna 2009; [3]Ferguson et al. 2001; [4,5]ISSG 2009; [6]Leung et al. 2002.

The economic impacts of invasive species are significant. For example, it is estimated that invasive species cost the United States economy $120billion per year (Pimentel et al. 2005) –

more than was spent on reconstruction on the Gulf Coast after the 2005 hurricane season (Hurricanes Katrina and Rita). Other nations presumably face a similar economic burden, although estimates at the national level have rarely been made. Ecological impacts arise when the desired functioning of an ecosystem is interrupted. Examples of this include the extirpation of native species (e.g. Ricciardi et al. 1998), and changes in forest structure caused by nitrogen fixing alien plants (Corbin & D'Antonio 2004). Finally, invasive species impact human health directly when they are infectious or pathogenic to humans, and indirectly by facilitating the transfer of human diseases. For example, the monkeypox virus directly affected human health when it infected 72 humans in the United States after being introduced in an infected Gambian pouched rat (Reed et al. 2004; See Box 5). An example of indirect human health effects from an alien species is the Asian tiger mosquito. This species has become invasive in many parts of the world and is an effective vector for several human diseases, including West Nile virus (Kutz et al. 2003).

Although invasive species are harmful by definition, it is important to note that a number of intentionally introduced species confer significant net benefits and that most unintentionally introduced species are a 'side-effect' of activities that otherwise yield positive net benefits. The horticultural trade is a case in point because it provides many economic and social benefits, but also introduces many harmful invaders. Moreover, many introduced species have both negative and positive impacts (Ewel et al. 1999; Knowler & Barbier 2005). The aquatic water hyacinth plant in Australia produces benefits for the horticultural trade when it is sold, and for consumers who appreciate having it in their ponds. However, it quickly becomes invasive when released, overgrowing waterways and requiring expensive eradication programs (Low 2001). Hence, to fully evaluate the impacts of alien species it is important to consider not just the damage they cause, but also their benefits. In what follows, though, we focus on the effect that invasive species have on the array of ecosystem services identified by the Millennium Assessment.

Invasive Alien Species and Ecosystem Services

Ecosystem services are the benefits that people obtain from ecosystems (Costanza et al. 1997, MEA 2005a). These include, for example, the provision of foods, fuels, fibers and fresh water, the cultural and religious benefits people get from their environment, and the regulation of water quantity and quality, disease, productivity and climate (see Box 3 for a more detailed description). Because invasive alien species alter the structure and function of ecosystems they have large impacts on the quality and quantity of services provided (MEA 2005, Lodge et al. 2006, Pejchar & Mooney 2009). In this section we discuss some of these impacts. Because the ecosystem services that support food security and human health are so critical to human welfare they are dealt with separately later in this paper.

Alien invasive species can have significant impacts on all of the provisioning services described in Box 3. Invasive plants, for example, reduce the quantity of water in rivers and groundwater when their transpiration rates are higher than those of native vegetation. This reduces water available to downstream communities (Pejchar & Mooney 2009; Box 4). Alien plants also reduce water availability if they grow so densely that access to water is impeded. In South-eastern Australia the invasive reed sweetgrass (*Glyceria maxima*)

overgrows streambeds to the extent that no exposed watercourse remains and livestock are unable to access water (Loo et al. 2009).

Table 3: Some ecological impacts of invasive species, organized by affected habitat. No part of this table is comprehensive. Rather, it is designed to give an idea of the range of taxa that become invasive, and the range of their ecological impacts.

Impact	Example
Forests	
Plants prevent forest regrowth after disturbance (e.g., logging, fire)	Cogon grass (*Imperata cylindrical*) is invasive in 73 countries where it infests degraded tropical forests, preventing tree growth
Plants outcompete native vegetation	Miconia (*Miconia convalescens*) overtakes native vegetation on many Pacific islands. Its shallow root system leads to landslides
Insects and fungal diseases infect tree species	Chestnut blight (*Cryphonectiria parasitica*) fungus has eliminated American chestnut trees, which were a dominant canopy species, from its native North American range
Oceans	
Marine organisms spread and establish large and dense populations	North Pacific Seastar (*Asterias amurensis*) is invasive in coastal waters of Australia where it consumes commercially valuable shellfish and negatively affects critically endangered fish species
	Caulerpa (*Caulerpa taxifolia*) is an aquarium strain of a marine alga. It grows as a monoculture across much of the Mediterranean, outcompeting native species and excluding other marine life, including commercially valuable fishes
Freshwaters	
Introduced predators reduce native biodiversity	Largemouth bass (*Micropterus salmoides*) has been introduced widely as a sportfish. It has extirpated populations of native fish where established
Invaders with broad habitat ranges	
Predators reduce populations of native animals	Indian mongoose (*Herpestese javanicus*) has been introduced widely to control pest rodents. It is a voracious predator that mostly consumes native mammals, birds, reptiles and amphibians, leading to extirpations and extinctions

Source for all examples is ISSG (2009).

Although less well understood, alien invasive species also have negative impacts on regulating ecosystem services, especially through their effect on species richness. Any

reduction in the diversity of species functional groups, for example, can reduce the capacity of an ecosystem to adapt when environmental conditions change. This implies a reduction in resilience – the main impact of a change in the regulating services (Perrings et al. 2010).

Box 3: Millennium Ecosystem Assessment Categories of Ecosystem Services

The Millennium Ecosystem Assessment (MEA) was a large scientific investigation into the contribution that different ecosystems make to human welfare. These contributions are known as 'ecosystem services', and the MEA report divided them into four categories as described below.

Provisioning Services are the products obtained from the environment, including fresh water and foods such as crops, livestock, fish from capture fisheries and aquaculture, and wild foods. Also includes the provisioning of fibers (e.g., cotton, hemp, silk and wood for fuel).

Regulating Services provide benefits through the regulation of ecosystem process, including climate regulation (e.g., evapotranspiration from forests creates rainclouds) water purification in wetlands, and ecosystem processes that regulate water flow and flooding (e.g., forest storage of rainfall). Ecosystems also regulate the presence and severity of diseases and pests, and provide pollinators for the crops that humans harvest.

Cultural services are the nonmaterial benefits obtained from the environment. These are often difficult to precisely define and quantify, but are extremely important for the creation and maintenance of societies. They include the many ways that natural ecosystems are incorporated into systems of belief and spirituality, the aesthetic benefits humans derive from the environment, and the pleasure and economic benefits from recreation and ecotourism.

Supporting Services do not provide direct benefits to humans, but are essential for the functioning of all other ecosystem services. These are the processes of soil formation, nutrient cycling and primary production. For example, crops could not be cultivated if there was no soil formation, and human wastes could not be processed in the environment without nutrient cycling.

Sources: MEA 2003, 2005a.

One of the most important regulating services for human welfare is the water purification provided by wetlands. Indeed, this service is recreated in sewage treatment and bioremediation plants all over the world. Invasive alien species can drastically reduce wetland biodiversity and nutrient cycling, resulting in lower water quality. For example, golden applesnail (*Pomacea canaliculata*) have been introduced to ponds and waterways across South East Asia. This species reduces macrophyte diversity and changes nutrient regimes to the extent that ponds shift from a clear-water, macrophyte dominated regime to a turbid, phytoplankton dominated regime (Carlsson et al. 2004; see also Box 7). Similarly, the common carp (*Cyprinus carpio*) is a widespread invader with severe implications for water quality. It is a benthivorous (bottom feeding) fish that reduces macrophyte biomass and

actively disturbs sediments while it feeds. This increases turbidity and decreases local and downstream water quality (Roberts et al. 1995).

By changing the structure and function of ecosystems alien invasive species can have major impacts on cultural services. This includes reductions in recreation opportunities, aesthetic enjoyment, spiritual satisfaction, and scientific and traditional knowledge. Impacts can come about from alteration of the mix of species in the system, the fire regime, the prevalence of pests and pathogens, or simply the degree to which the system is regarded as dangerous or benign. The invasion of the Burmese python (*Python molurus bivittatus*) into the Florida Everglades, for example, is expected to have an effect on peoples' perceptions of that system and the benefits it offers visitors (Rodda et al. 2009). It is reasonable to expect that many people will choose not to visit the Everglades now that a large constrictor snake is established there.

Box 4: Working for Water – Invasive Alien Species and Water Availability in South Africa

South Africa is heavily invaded by alien plants. Many of these alien species transpire more water than native plants, leading to an estimated 7% decrease in runoff across South Africa as a whole (Versfeld et al. 1998). This represents a significant decrease in water flowing to downstream communities and towns, many of which are already water-stressed.

The Working for Water program was established in 1995 with the twin goals of reducing water loss to invasive plants and creating jobs for economically disadvantaged communities (Marais & Wannenburgh 2008). The program hires workers to locate and cut down stands of invasive vegetation, especially when that vegetation is located along watercourses. Enormous success has been achieved in terms of employment, with the program providing up to 30,000 part time jobs each year. Invasive species have been cleared from 1.6 million hectares at a cost of 116 million Rand, resulting in increased annual water yields of an estimated 34.4 million cubic meters. The Working for Water program is a more economical way to increase water availability than other options such as dam construction (Marais & Wannenburgh 2008).

Finally, invasive species affect the supporting services – the ecosystem processes – that support the production of all other services. For example, plant invasions can increase or decrease carbon storage, depending on the morphology and turnover rates of the native and invasive species (Pejchar & Mooney 2009). Loss of forest to fire-tolerant grasses, for example, will dramatically decrease carbon storage, while invasion of trees into grasslands will have the opposite effect.

Invasive Alien Species and Human Health

Alien species affect human health in at least three ways. First, the organisms that cause many human diseases, such as SARS and HIV/AIDS, are alien invasive species that have become

established beyond their native range. Second, invasive alien species can act as vector organisms for the spread and transmission of human diseases. The spread of West Nile Virus in the United States, for example, has been much more rapid and damaging because the invasive Asian tiger mosquito (*Aedes albopictus*) has proven an effective transmission vector (Juliano & Lounibos 2005). Third, invasive alien species can impact human health indirectly by reducing food security and production, or by reducing the production of safe drinking water and other ecosystem services. Impacts on food security are dealt with in the following section, impacts on water supply, water purification and other ecosystem services were dealt with in the previous section. Here, we concentrate on the role of invasive alien species either as direct infectious agents, or as the vectors of infectious agents.

Invasive Alien Species That Directly Infect Humans

History is replete with examples of alien invasive diseases that have spread widely with enormous impacts on human health (Wilson 1995). These include smallpox, measles, schistosomiasis and tuberculosis, each of which has caused high levels of mortality and/or morbidity, and some of which have devastated whole civilizations (McMichael & Bouma 2000). During the 20th Century enormous advances have been made in the identification and treatment of infectious diseases, and in sanitation measures, such as separated sewers and water supplies, that can prevent and contain outbreaks (Weiss & McMichael 2004). Developed countries in particular have seen large declines in mortality rates from infectious diseases. In Chile, for example, the percentage of deaths caused by infectious diseases dropped from 46.6 to 20.9 between 1909 and 1999 (Weiss & McMichael 2004). Less developed countries, however, continue to bear a disproportionate burden from alien invasive diseases. In Zambia, for example, ~30% of people contracting measles die from the disease, while in London the death rate is <1% (Delfino & Simmons 2000).

Against the advances in disease treatment is the increasingly rapid movement of humans, animals and cargo across the globe. This has increased potential rates of disease spread by orders of magnitude compared to a century ago. Infected humans traveling on commercial aircraft can spread diseases across the globe within days, as occurred in the case of the global SARS outbreak of 2003. The first international spread of the disease occurred soon after February 21, when 12 guests at a Hong Kong hotel became infected. These people then traveled to Singapore, Vietnam, Canada, the United States and Ireland, causing outbreaks in all of these except Ireland. This spread occurred just months after the disease is presumed to have made the jump from wild animals to humans, and before the infectious agent causing the disease had been identified (Mahmoud & Lemon 2004). Contrast this with previous modes of travel and trade, such as sailing ships, and it is clear that globalization has created pathways and vectors capable of moving diseases more rapidly than outbreaks can be identified and contained.

At the same time that globalization has increased the risks for rapid spread of disease, the number of emerging infectious diseases (EIDs) has increased (Jones et al. 2008). EIDs are defined as diseases of humans that have recently appeared, increased in incidence, or that threaten to do so in the near future. There are at least 1,415 species that cause diseases in humans, including bacteria, viruses, fungi, protozoa and helminthes (Taylor et al. 2001).

Zoonotic diseases (those that can be transferred from animals to humans) make up 61% of the total number, and appear to be of increasing importance because they make up 75% of recent EIDs (Taylor et al. 2001). Thus, a major challenge for public health is the identification and isolation of these diseases before they become widespread. This challenge is made all the more difficult by the huge range of vectors that can transport potentially diseased humans and animals. As new threats emerge, pathways that appeared to be benign can become highly risky. This has been the case for the global trade in live poultry, which has become the dominant pathway for the spread of the recently emerged H5N1 avian influenza (Kilpatrick et al. 2006).

There are very real economic reasons to be concerned about EIDs. The rapid emergence and spread of the SARS virus during 2002-03 caused a major medical response, cancellation of travel, decreases in exports from affected countries, and many other economically damaging outcomes. In total, the global economic impact of the virus was estimated to be approximately $US40billion (Lee & McKibbin 2004). Other diseases, such as the current H1N1 swine flu pandemic, HIV and monkeypox have the potential to be at least as economically damaging (see Box 5).

Box 5: Monkeypox introduced to United States through the pet trade

Monkeypox is a viral disease endemic to central and western Africa. It was first identified in 1958 in laboratory primate populations, and has since been found to be carried by a range of African rodents, including the Gambian pouched rat (Cricetomys gambianus). The first record of a human infection from this emerging infectious disease occurred in 1970 (CDC 2003), and prior to an outbreak in the U.S. during 2003 the disease had never been recorded on humans outside of Africa.

Although they are now banned from import, the pet trade in the U.S. previously introduced and sold the Gambian pouched rat. In 2003 people across the Midwest began to report unusual rashes and fevers. A rapid response by the Centers for Disease Control established that all of the diseased people had purchased pet prairie dogs from a single retailer. These prairie dogs had been kept with a Gambian pouched rat that was infected with monkeypox when it was imported from Africa (CDC 2003). A total of 72 humans became ill during the disease outbreak (Reed et al. 2004). Rapid identification of the disease and tracing of its source was important because of the potential for the disease to become established in wild native prairie dog populations, or in populations of other rodents. This would have created a permanent reservoir of monkeypox in North America, and the potential for many more human infections.

Invasive Alien Species Acting as Vectors for Human Diseases

The introduction, establishment and spread of alien animals that act as disease vectors has serious implications for human health. The Asian tiger mosquito (Aedes *albopictus*) is native

to Asia but now established as an invader in at least 28 countries (Benedict et al. 2008). The dominant pathway for its spread is the global trade in used tires, which often contain small pools of water in which mosquito eggs are transported (Reiter 1998). The continuing global spread of this species is of particular concern because it acts as a vector for many human diseases, including West Nile Virus, dengue virus, Japanese encephalitis and yellow fever (Benedict et al. 2007). In the United States the Asian tiger mosquito has been an important vector for the spread of the recently introduced West Nile virus (Kutz et al. 2003). In this way it is an alien invader that is facilitating the spread of another alien invasive species.

Rats and other rodents are widely invasive and act as reservoirs for many human diseases. The bubonic plague spread across Europe and Asia in repeated pandemics. Black rats (*Rattus rattus*) were the main reservoir for this disease and were widespread across Europe as an invasive species. The plague spread through the rat population and was then transmitted to humans via ticks that bit an infected rat and then a human. Bubonic plague was thus able to spread across Eurasia on a widely invasive rodent species, decimating human populations and economies (McMichael & Bouma 2000). A contemporary example of rodents acting as the reservoir for a human disease is the introduction of monkeypox to North America on an infected pet Gambian pouched rat (see Box 5).

Invasive Alien Species Impacts on Food Security

Food security (Box 6) is an essential part of human welfare. Foods are harvested from agriculture, hunting and gathering, and from aquaculture and capture fisheries. The Millennium Ecosystem Assessment noted that production of foods from agriculture and aquaculture had both increased substantially during the last half century, largely through intensive plant breeding programs, advances in agrochemical use (e.g., fertilizers, pesticides), and an increased global aquaculture industry. In contrast, the MEA found that production of foods from wild living resources has declined (MEA 2005b). The primary causes of this decline are loss of natural areas and unsustainable harvesting of wild populations. The total effects of alien species on populations of wild harvested foods are poorly known, but are presumably large because of the many ways that alien species alter ecosystems and animal and plant populations. In what follows we discuss the impacts of alien invasive species on agriculture because this produces by far the greatest proportion of total human foods, and because little information is available about impacts on other food sources.

It is worth noting that most worldwide food production is from alien species. For example, wheat is native to a region known as the ‘fertile crescent’, a relatively small area of the Near East. Despite its small native range, wheat is one of the world’s most important crops and is grown across North America, Europe, Australia, Asia and South America. All other major global crops and livestock species have similarly been exported from their native ranges and are now cultivated elsewhere. These species increase human welfare and improve food security. In this section we are not concerned with beneficial alien species. Instead, we are interested in the many alien species that increase the costs and/or reduce the yields of agriculture.

Box 6: Definition of food security, and relationship to food production and development status

A number of alternative definitions of food security have been proposed (see Pinstrup-Andersen 2009 for a review). The most widely used is that of the Food and Agriculture Organization, which states that "food security exists when all people, at all times, have physical and economic access to sufficient, safe and nutritious food to meet their dietary needs and food preferences for an active and healthy life" (FAO 1996).

Food production is closely related to food security, and is a measure of the quantity and quality of food resources that are harvested from cultivated (i.e., crops and livestock) or wild (i.e., wild plants and game) systems. The extent to which food production and food security overlap for a nation depends in part on whether food is produced in excess of the nation's dietary needs. Crop failures in a nation that consumes most of its food production automatically lead to a decline in food security. This close relationship between food production and food security is most likely to occur in developing nations with a high proportion of subsistence farmers (Perrings 2007). In contrast, a nation that exports most of its agricultural production could see large crop failures without an impact on the food security of its citizens, assuming it was able to reduce its exports.

Since the beginnings of agriculture, alien invasive species have impacted food yields, with common pest taxa ranging from insects, nematodes and rodents to viruses, bacteria, fungi and weeds (Oerke 2006). Agricultural invaders reduce food security by diminishing the quality, quantity and/or reliability of the yield. Some of the best known examples of crop failures due to invasive pathogens come from 19th century Europe. The potato blight (*Phytophthora infestans*) caused widespread failure of the potato crop across Europe, and the subsequent Irish famine (Bourke 1964). Phylloxera destroyed the vines of Europe effectively halting wine production for 25 years in the latter part of the century (Campbell 2005). Rinderpest, a cattle disease from the steppes of Asia, had been periodically introduced and reintroduced in Europe as a side effect of war since the 1700s. The advent of rail transport in the 19th century and the transport of cattle it enabled caused an outbreak from 1857 to 1866 that denuded Europe of cattle (Roeder et al. 2004).

At a global scale, contemporary crop losses to weed, animal, pathogen and virus pests are substantial. Oerke (2006) has calculated percentage losses due to the pests of six major crops: wheat – 28; rice – 37; Maize – 31; potatoes – 40; soybeans – 26; cotton 28. Importantly, these are crop losses after efforts have been made to control the pest species – losses would be far larger in the absence of those control efforts. We note that the figures just given are for the impacts of all pests, native and alien, on these crops. The

origins of many pests, especially diseases, are poorly known, making it impossible to definitively determine the contribution of alien invasive species to global losses. It is known, however, that alien species cause the bulk of losses, especially those from pathogens and viruses that are often introduced accidentally with crop germplasm.

Virtually all agriculture involves some level of pest suppression. Native pests, such as the elephant populations in Cameroon that raid and trample crops (Tchamba 1996), are difficult to avoid and it may not be desirable to reduce their populations. In contrast, the majority of agricultural pests are alien species. These cause significant losses in food production and there is good reason to control them with the aim of avoiding their impacts. Where pest control is possible it is often expensive and may involve the construction of fences or other barriers, use of herbicides or pesticides and/or changes in planting and growing schedules so that production is out of sync with pest life-cycles. Each of these can be expensive and will lead to financial losses for farmers. In most cases, the invasive species also reduce agricultural yield because it is rarely feasible to entirely eliminate their effects.

Efforts to mitigate the impacts of invasive alien species, and the yield losses these species cause, lead to economic losses. It is estimated that the annual cost of the herbicides used to control alien invasive plants on Australian farmland is around $1.5billion (Australian) per year (Sinden et al. 2004). In addition, alien invasive plants are estimated to cause agricultural yield losses in Australia with an annual value of $2.2billion (Sinden et al. 2004). In California, the invasive yellow star-thistle (*Centaurea solstitialis*) plant infests at least 14.3million acres of rangeland. It is not palatable to livestock and reduces livestock yields by 13-15%. The economic costs from this reduced agricultural output in California have been estimated at $17.1million per year (Eagle et al. 2007).

Although they have rarely been studied and economically quantified, the impacts of invasive alien species on agriculture in developing nations are also high. The Indian myna (*Acridotheres tristis*), a bird introduced to Africa to control pest insect populations, has spread widely and now damages grape and other fruit crops. It also reduces biodiversity by outcompeting native birds for nesting sites (Chenje & Mohamed-Katerere 2006). Across South-east Asia the invasive golden apple snail has reduce rice harvests (see Box 7). Because agricultural production in developing nations is more closely linked to immediate issues of food security, the impacts of invasive alien species are more consequential to human welfare (Perrings 2007; Box 6).

In some cases the control costs of invasive species become so high that it is no longer economical to farm infested land. Land abandonment can occur when fire-tolerant grasses invade, changing the fire regime so that forests, and the shifting slash-and-burn agricultural systems they support, are lost (Albers & Goldbach 2000). This has been the case in some parts of Mexico where invasive bracken fern (*Pteridium aquilinium*) has so altered patterns of fire, ecological succession and soil fertility that farmers have abandoned invaded areas (Schneider & Geoghegan 2006). This reduces food production

(unless the farmers are able to substitute other land) and can impose high cultural costs because traditional farming techniques are no longer practiced.

Box 7: Golden apple-snail impacts on food production and security

The golden apple-snail (*Pomacea canaliculata*) is a large snail native to South America. It has become established as an invader in several regions of the world, including South-East Asia, where it was introduced intentionally as a low-cost, high-protein domestic food source, and to create an export market for escargot (Joshi 2005). Here, we discuss the experience with this species in the Philippines.

Golden apple snail was intentionally introduced to the Philippines in 1982 (Joshi 2005). Its introduction was strongly promoted by the Philippine Department of Agriculture which believed it would be a valuable and easily cultivated agricultural product that could improve rural livelihoods (Anderson 1993). Although originally introduced into contained settings such as concrete ponds, golden apple-snail escaped and by 1986 was considered a serious agricultural pest (Joshi 2005). The speed of its escape and establishment in the wild was hastened because farmers did not find the snails palatable and no export markets emerged. Many farms were simply abandoned.

The largest impact of golden apple-snail in the Philippines, as in other parts of Asia, is its consumption of rice. When rice is direct seeded (i.e., grown from seed in the paddy) it is susceptible to golden apple-snail grazing for up to four weeks after seeding. Transplanted rice is susceptible for up to two weeks. Experimental studies show that yield losses from golden apple-snails range from 20% in paddies with an infestation of 1snail/m2 to 90% in paddies with infestations of 8snails/m2. The economic losses from reduced rice production during 1990 were estimated to be in the range $US28-45million, and eventual costs from this invasion may be as high as $US1.2billion (Naylor 1996). All rice-growing areas of the Philippines are now infested with golden apple-snail (Joshi 2005) and there is little chance that it could ever be eradicated.

4 INTERNATIONAL POLICY OPTIONS FOR MANAGING THE RISKS POSED BY ALIEN INVASIVE SPECIES

Preventing the spread and impacts of invasive alien species is an international public good that requires coordination among nation states. The greatest protection from invasive species would occur if each nation made efforts to prevent potentially harmful species from leaving its territory. This principle is included in the Convention on

Biological Diversity (CBD) which gives signature nations "the responsibility to ensure that activities within their jurisdiction or control do not cause damage to the environment of other States or of areas beyond the limits of national jurisdiction" (Article 18). Yet few countries commit resources to reducing the risk they pose to others, and those that do are primarily motivated by the threat of retaliation if they do not.

The challenge for policy-makers and managers is to maintain the benefits of globalization while limiting the rates of introduction, establishment and spread of alien invasive species. The 168 countries that have signed the Convention on Biological Diversity (CBD) have agreed to not expose other countries to environmental risks such as alien invasive species, and to "prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species" (Article 8(h)). Progress toward these goals differs greatly by country, as does the level of resources allocated. Programs to limit the spread of infectious diseases of humans are by far the most advanced, with the Centers for Disease Control and World Health Organization providing international support and capacity to rapidly respond to new outbreaks. By contrast, most other classes of alien invasive species are managed at the national level. Indeed, international coordination of disease control in non-human diseases is limited to a few particularly severe animal diseases, such as Rinderpest. Yet the international coordination of national efforts is a pre-requisite for mitigating the invasive species risks from trade and trade growth.

To identify the policy and management options associated with distinct alien species categories, we distinguish between four classes of invasive alien species. First, as mentioned above, there are relatively advanced programs in place at the international level for human diseases. Second, the 174 member nations of the World Organisation for Animal Health (OIE) have agreed to report outbreaks of animal diseases, mostly diseases of livestock, to a central database. This process allows nations to track diseases and to adjust the products and livestock that they allow for import accordingly. Third, invasive alien diseases of crops are often the focus of quarantine inspections at national borders (but this varies by country). Fourth, alien species that do not affect human health and are not diseases of major crops are generally traded without inspection or efforts to prevent the arrival and establishment of invaders.

In the next section we describe current international programs for preventing the spread of alien human diseases, and how these could be improved by increasing capacity in poorer 'weak-link' countries. Because the other categories of invasive alien species are generally managed at the national level we then discuss how vectors of introduction can be managed, and the potential benefits from international cooperation. We conclude with a set of specific recommendations for reforming international policy that could reduce the global introduction, spread and impacts of alien invasive species. Figure 1 summarizes many of our recommendations for how the global spread of invasive species can best be mitigated.

International Programs for Managing Emerging Human Diseases

The procedures and capacity for both identification and containment of emerging infectious diseases (EIDs) are better in high-income than in low-income countries. There are a number of reasons for this. One is that diseases transmission rates are generally higher in poor countries. Poorer countries have social conditions, such as lack of sanitation and crowded settlements that encourage disease emergence and spread. A second is that a greater proportion of the population in low-income countries is located in rural areas, and hence is more likely to be in close contact with wild animals that carry and transmit zoonotic diseases to humans. A third is that the resources available for inspection and interception of infected individuals from abroad is more limited, making poor countries more vulnerable to diseases imported from other countries. All of these have contributed to higher rates of emergence and re-emergence of human diseases in poorer countries (Jones et al. 2008). This is of concern to those countries where diseases are emerging, but also to all other countries because of the risks posed by trade and travel with infected countries.

The 2005 International Health Regulations (IHR) administered by the World Health Organization (WHO) mandate cooperative international action to address the human health risks posed by trade and travel-related disease introductions. A central tenet of the IHR (2005), embodied in Articles 6 and 7, is that member countries are required to notify the WHO of any event that may have implications for international health. More particularly, Article 9 requires notification of any international public health risk due to the movement of people, disease vectors or contaminated goods. The WHO is then mandated to take precautionary action on behalf of the international community to mitigate the risks posed by the disease (Perrings et al. 2010).

Figure 1: Potential intervention points in the international transport of invasive alien species. The left column shows a modified version of the invasion sequence (see Box 1). The right column lists actions that could be followed by the international community to reduce the chance for species spread. Not all countries will have the capacity to follow all steps in the right hand column. In these cases, the international public good will be best served through technical, institutional and financial assistance from developed to less developed nations. See text for more detail.

Species in native range

1) Assess risks posed by species, and where (globally) it would have impacts
2) Determine which vectors could transport species
3) Publicize risks, especially to trading partners in regions where species could become invasive
4) Manage high risk vectors to limit potential for species transport
5) Modify trades or trade practices as necessary to reduce risks of species spread

↓

Species in vector

1) Monitor vectors for high risk species (e.g., quarantine inspections)
2) Manage vectors to reduce chance of species transport (e.g., ballast water exchange)
3) Survey likely sites of introduction (e.g., high traffic ports) for species

↓

Species Introduced/established beyond native range

1) Eradicate populations where feasible
2) Limit invasive species spread
3) Notify international community of species range expansion
4) Re-assess risk of species and its transport, inform international community of results and modify trade practices as necessary to reduce risk of further spread
5) Repeat previous step as necessary if species continues to spread

In the case of SARS, for example, the World Health Organization (WHO) was successful at coordinating an effective international response. Although the disease ultimately spread to a large number of countries, it was rapidly identified and infected fewer than 10,000 people before being contained (Mahmoud & Lemon 2004). Many of the impacts of SARS could have been avoided, however, if better systems had been in place in China, where the disease first appeared, to identify and quarantine infected people.

Air travel is the fastest pathway for the spread of human diseases. The procedures that would be required to eliminate this pathway of spread – quarantining all passengers for long enough to be sure they are not carrying a disease – are impractical and carry very high costs. Instead, the approach most often taken by nation states is to wait until a disease emerges elsewhere, and then to rapidly mitigate the risk that it will be transmitted to them, often by quarantining arriving passengers or canceling flights. Given the centrality of trade and travel to economic activity, this is likely to remain the main method used by countries to contain diseases. It was largely effective for controlling SARS, but has been much less effective for other diseases, such as HIV/AIDS and the current H1N1 swine flu pandemic.

In the future, the greatest advances for preventing the outbreak and spread of EIDs are likely to come from implementing three different types of programs. Importantly, each of these requires international cooperation and capacity building in weak-link countries. First, efforts to prevent EIDs from entering the human population will need to focus on sanitation within low-income countries, along with education about the potential disease risks from domestic and wild animals. Second, early detection of new EIDs would allow responses to be enacted before the disease has a chance to spread. This will require additional basic medical services in the countries and regions where EIDs are most likely to emerge. This also implies developing the capacity of low-income countries to defend their borders against the transmission of diseases. Finally, and most importantly, for those diseases that do emerge and begin to spread, international cooperation to rapidly implement controls on air travel, and other pathways of spread, are required (Delfino & Simmons 2000; Fraser et al. 2009). Preventing and containing EIDs is a clear case where the international public good is best served by taking a global view of the problem, rather than by countries allocating all their efforts to protecting their own borders.

Managing Vectors of Introduction

Under the World Trade Organization (WTO) and its constituent agreements, particularly the General Agreement on Tariffs and Trade (GATT) and the Sanitary and Phytosanitary (SPS) Agreement, countries have the right to take actions to protect food safety and animal or plant health. Unlike human diseases, however, these agreements authorize only national defensive measures, and do not authorize collective coordinated action to mitigate animal and plant disease risks. This leaves individual nations to manage the risks from intentional and accidental vectors of alien species introduction.

Vectors of intentional species introduction include the pet and aquarium trades, the nursery plants trade, the live food trade (Keller & Lodge 2007), and the international livestock trade (see Table 1 & Box 2). Species transported are pre-selected for desirable attributes, and the trades provide many economic and social benefits. Intentionally introduced species also often become invasive, or transport with them other invasive species (Jeschke & Strayer 2005). Because these vectors introduce beneficial as well as invasive species there have been growing efforts to develop tools for determining the invasion risks posed by individual species. It is widely accepted (Lodge et al. 2006, IUCN 2000) that the best way to reduce the risks of invasions from intentional vectors of introduction is to assess the risk of each species in transport and prevent the introduction of those that are considered to have a high risk of invasion. This approach can yield economic benefits for importing countries (Keller et al. 2007), along with the environmental, social and agricultural benefits from fewer invasions.

Application of these risk assessment tools holds the promise of allowing beneficial species and directing limited resources to preventing the introduction of high-risk species. The most prominent tool yet developed for risk assessment of intentionally introduced species is the Australian Weed Risk Assessment (WRA) (Pheloung 1995).

Australian government scientists developed this tool in the early 1990s. In 1997 it was introduced as a mandatory screening tool for all new plant species proposed for introduction to Australia. If a species is assessed as posing a high risk of becoming invasive it is not allowed for import. The WRA has been demonstrated to have good accuracy across a range of geographies (Gordon et al. 2008) and has been adopted in a modified form by New Zealand.

Species that arrive accidentally are not expected to provide benefits, but they do have a non-zero probability of causing harm. The number and magnitude of vectors makes preventing accidental introductions an enormous challenge. For example, the global ship fleet includes at least 94,000 large vessels and moves most international trade (IMO 2007). Each ship poses a risk of introducing new alien species every time that it docks. This risk comes from organisms entrained in ballast water, attached to hulls, or in the actual cargo carried. It is unlikely that any country will ever commit the resources required to fully inspect arriving ships. Similar issues arise for other vectors, such as the potential for airline passengers to inadvertently carry invasive species in their baggage (e.g., seeds attached to dirty shoes).

The lack of expected benefits from vectors of unintentional species introduction means that they can be managed to simply remove organisms from transport. Here, we describe two standards that have been developed to restrict the spread from this type of vector. The first is the international ISPM 15 standard for treatment of wood and wood packaging, developed in response to the large number of forest pests that have been inadvertently spread in untreated wood. Signatory nations agree to treat wood packaging material (e.g., wooden palettes) prior to export to ensure that they do not contain pests.

The second example is a national policy that could be adapted for an international context. The U.S. Plant Protection Act requires that all plants transported to the U.S. be accompanied by a phytosanitary certificate. This certificate must be completed by plant health inspectors in the exporting country and must attest that plants are not contaminated with invasive diseases or pests. This program is consistent with U.S. obligations as a signatory to the WTO's SPS Agreement (Hedley 2004). If this standard was internationally adopted it would provide greater protection to the U.S. because its trading partners would be less likely to become invaded. It would also provide protection to other nations. There is currently no international body that could implement such standards.

Although the number of risk assessment tools and national/international import standards continues to increase, at a global scale they are still rare and limited to developed countries. Further developing and applying tools and standards for international pest and disease risks could serve a double purpose. On the one hand, by making information on invasive species risks generally available it could allow countries to make more effective use of existing defensive measures, such as the SPS Agreement. On the other, it could form the basis for coordinated international action. It would support greater international cooperation in preventing the spread of invasive alien species. There is presently no

international organization that could either develop or implement such tools/standards, but the potential benefits it would offer warrant serious attention (Perrings et al. 2010). In particular, it would help to reduce the gap in invasive species information and management capacity between developed and developing countries, and would thus help to address the 'weakest-link' problem in the spread of alien species.

The World Trade Organization and Regional Trade Agreements

A primary goal of the World Trade Organization (WTO) and the increasing number of regional trade agreements is to eliminate barriers to free trade. As countries become more open to imports they also increase the risk of arrival of new invasive species (Dalmazzone, 2000; Vilà and Pujadas, 2001, Ricciardi 2006). We have noted that under WTO rules a country is allowed to restrict the import of products in order to prevent the introduction of a potentially harmful species, although the WTO implements a high bar to justifying such restrictions, with the requirement for the country limiting trade to provide scientific evidence that the restrictions are justified (Perrings et al. 2010). Since invasive species risks are an externality of trade in international markets, the first best policy for addressing them is to internalize the externality – to confront those whose behavior is the source of harm with the full cost of their actions. The difficulty with this is that any action by one country that imposes explicit or implicit tariffs on imports from other countries is seen as a form of protectionism, and may therefore be in violation of the terms of the General Agreement on Tariffs and Trade, the legal instrument of the WTO. There are four main options for addressing this problem.

1. *Harmonization of the IHR and SPS Agreements*. This should bring the SPS Agreement into conformity with the IHR, and simultaneously bring the World Animal Health Organization (OIE) into conformity with the WHO (Perrings et al. 2010). This is necessary if the international community is to be able to take collective action on the control of trade-dispersed pests and pathogens affecting all species, i.e. to internalize the global externalities of trade. Given the very tight relation between human and animal pathogens (most emerging infectious diseases are zoonoses, animal diseases that cross over into the human population) there is an advantage in harmonizing the two agreements just from a human health perspective. But it would also allow for collective action on a range of agricultural and environmental pests and pathogens. This option does involve renegotiation of an international instrument, however, and so is only a potential solution in the longer term. In the meantime there is still the problem that many countries are currently underserved by existing mechanisms.

2. *Develop a global monitoring and evaluation system for invasive pests and pathogens*. If countries are to use the options currently open to them under the SPS Agreement, they need to have the capacity to identify and estimate the risks posed by potentially invasive species. At present this requirement favors countries with that capacity and penalizes the rest. Rich countries make disproportionately high use of the provisions of the SPS

Agreement. Poor countries make disproportionately low use of these provisions. A global monitoring and evaluation system could ensure that the provisions of the Agreement were used in a systematic way. A number of existing institutions have international monitoring functions, and there are a number of efforts to build global environmental monitoring systems by networking existing facilities. Both might be used to support such an effort. Adding the assessment of the globally distributed risk posed by individual species would enable it to serve the SPS Agreement.

3. *Use the environmental provisions of existing and proposed Regional Trade Agreements (RTAs) to address invasive species risks within regional trade areas*. There are over 400 RTAs either already in force or notified to the WTO. Many have environmental committees. While a number of these committees are ineffective, there are a least some with the capacity to identify and address the costs imposed by the trade-related dispersal of pests and pathogens within the regional trade area. Because many RTAs cover contiguous or neighboring countries that are bioclimatically similar, and because they are designed to encourage the free flow of goods and services between member states, they can also accelerate the movement of potentially harmful species between member states. It is the role of environmental committees to identify actions to mitigate the associated risks. Guidelines on this function, supported by information on emerging international threats, would enable the RTA environmental committees to be more effective.

4. *Intensify inspection at key international nodes*. While the world trade network is very tightly linked, there are nodes that are of particular importance for the redistribution of species. For example, Amsterdam has historically been especially important in the distribution of horticultural species, widely recognized to be a principal source of many of the pests and pathogens that have been most damaging to both the commercial production of foods, fuels and fibers, and to plant communities outside of agroecosystems. Other cities play a similar role for the trade in live animals or birds. There are also common transit points for marine traffic - the Panama and Suez Canals for instance – that provide inspection opportunities. Globally funded inspection efforts at such nodes would provide significant international benefits, and would support an early warning system on emerging threats

REFERENCES

Albers HJ & Goldbach MJ. 2000. Irreversible ecosystem change, species competition, and shifting cultivation. *Resource and Energy Economics* 22: 261-280.

Anderson B. 1993. The Philippines snail disaster. *The Ecologist* 23:70-72.

Bampfylde CJ, JA Peters & AM Bobeldyk. 2009. A literature analysis of freshwater invasive species research: are empiricists, theoreticians and economists working together? *Biological Invasions* DOI 10.1007/s10530-009-9540-2

Benedict MQ, RS Levine, WA Hawley and LP Lounibos. 2007. Spread of the tiger: global risk of invasion by the mosquito Aedes albopictus. *Vector Borne and Zoonotic Diseases* 7:76-85.

bij de Vaate A, K Jazdzewski, HAM Ketelaars, S Gollasch & G Van der Velde. 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1159-1174.

Bourke PMA. 1964. Emergence of potato blight, 1843-46. *Nature* 203:805-808.

Campbell C. 2005. *The Botanist and the Vintner: How Wine Was Saved for the World. Algonquin Books*. Chapel Hill, North Carolina, USA.

Carlsson NOL, C Brönmark & L-A Hansson. 2004. Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology* 85:1575-1580.

Carlton JT & Geller JB. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. *Science*. 261:78-82.

CDC [Centers for Disease Control]. 2003. *Preliminary report: multistate outbreak of monkeypox in persons exposed to pet prairie dogs*. Available at: http://www.cdc.gov/ncidod/monkeypox/report060903.htm

Chenje M & J Mohamed-Katerere. 2006. Invasive alien species. Pages 331-347 in *Africa Environment Outlook 2*. United Nations Environment Program.

Coates P. 2006. *American perceptions of immigrant and invasive species: Strangers on the land*. University of California Press, Berkeley, CA.

Corbin J, & CM D'Antonio. 2004. Effects of exotic species on soil nitrogen cycling: Implications for restoration. *Weed Technology* 18:1464-1467.

Costanza R, R d'Arge, R de Groot, S Farberk, M Grasso, B Hannon, K Limburg, S Naeem, RV O'Neill, J Paruelo, RG Raskin, P Sutton & M van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Science* 387:253-260.

Costello C, M Springborn, C McAusland & A Solow. 2007. Unintended biological invasions: does risk vary by trading partner? *Journal of Environmental Economics and Management* 54:262-276.

D'Antonio CM, J Levine & M Thomsen. 2001. Propagule supply and resistance to invasion: A California botanical perspective. *Journal of Mediterranean Ecology* 2:233-245.

Daily GC, G Ceballos, J Pacheco, G Suzan & A Sanchez-Azofeifa. 2003. Countryside biogeography of neotropical mammals: Conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* 17:1814-1826.

Dalmazzone S. 2000. Economic factors affecting vulnerability to biological invasions. Pages 17-30 in C Perrings, M Williamson and S Dalmazzone (eds) *The Economics of Biological Invasions*. Edward Elgar, Cheltenham.

Darrigran G & C Damborenea. 2005. A South American bioinvasion history: Limnoperna fortunei (Dunker, 1857), the golden mussel. *American Malacological Bulletin* 20:105-112.

Daszak P, AA Cunningham & AD Hyatt. 2000. Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science* 287:443-449.

Dehnen-Schmutz K, J Touza, C Perrings & M Williamson. 2007. A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions* 13:527-534.

Delfino D & PJ Simmons. 2000. Infectious diseases as invasive in human populations. Pages 31-55 in C Perrings, M Williamson & S Dalmazzone (eds) *Economics of Invasive Species*. Edward Elgar, Cheltenham.

Dobson A, I Cattadori, RD Holt, RS Ostfeld, F Keesing, K Krichbaum, JR Rohr, SE Perkins & PJ Hudson. 2006. Sacred cows and sympathetic squirrels: the importance of biological diversity to human health. *PLOS Medicine* 3:714-718.

Drake JM & CL Jerde. 2009. Stochastic models of propagule pressure and establishment. Pages 83-102 in Keller RP, Lodge DM, Lewis MA and Shogren JF (eds) *Bioeconomics of Invasive* Species. Oxford University Press, New York.

Drake JM & DM Lodge. 2006. Allee effects, propagule pressure and the probability of establishment: Risk analysis for biological invasions. *Biological Invasions* 8:365-375.

Drake JM & RP Keller. 2004. Environmental justice alert: do developing nations bear the burden of risk for invasive species? *BioScience* 54:718-719.

Duncan RP, M Bomford, DM Forsyth & L Conibear. 2001. High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. *Journal of Animal Ecology* 70:621-632.

Eagle AJ, ME Eiswerth, WS Johnson, SE Schoenig & GC van Kooten. 2007. Costs and losses imposed on California ranchers by yellow starthistle. *Rangeland Ecology and Management* 60:369-377.

Elton CS. 1958. *The ecology of invasions by animals and plants*. University of Chicago Press, IL, USA.

Ewel JJ, DJ O'Dowd, J Bergelson, CC Daehler, CM D'Antonio, LD Gomez, DR Gordon, RJ Hobbs, A Holt, KR Hopper, CE Hughes, M LaHart, RRB Leakey, WG Lee, LL Loope, DH Lorence, SM Louda, AE Lugo, PB McEvoy, DM Richardson & PM Vitousek. 1999. Deliberate introductions of species: Research needs - benefits can be reaped, but risks are high. *Bioscience* 49:619-630.

FAO (Food and Agriculture Organization). 1996. *Rome declaration on world food security*. http://www.fao.org/docrep/003/w3613e/w3613e00.HTM. Accessed August 13, 2009.

Ferguson NM, CA Donnelly & RM Anderson. 2001. The foot and mouth epidemic in Great Britain: pattern of spread and impact of interventions. *Science* 292:1155-1160.

Finnoff DC, Settle C, Shogren JF and Tschirhart J. 2009. Integrating economics and biology for invasive species management. Pages 25-43 in Keller RP, Lodge DM, Lewis MA and Shogren JF (eds) *Bioeconomics of Invasive Species*. Oxford University Press, New York.

Fischer J, DB Lindenmayer & AD Manning. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment* 4:80-86.

Flannery T. 2006. *The weather makers: How man is changing the climate and what it means for life on earth.* Atlantic Monthic Press, New York, NY.

Fraser C, CA Donnelly, S Cauchemez, WP Hanage, MD Van Kerkhove, TD Hollingsworth, J Griffin, RF Baggaley, HE Jenkins, EJ Lyons, T Jombart, WR Hinsley, NC Grassly, F Balloux, AC Ghani, NM Ferguson, A Rambaut, OG Pybus, H Lopez-Gatell, CM Alpuche-Aranda, IB Chapela, EP Zavala, DME Guevara, F Checchi, E Garcia, S Hugonnet & C Roth. 2009. Pandemic potential of a strain of influenza A (H1N1): early findings. *Science* 324:1557-1561.

Gordon DR, DA Onderdonk, AM Fox & RK Stocker. 2008. Consistent accuracy of the Australian weed risk assessment system across varied geographies. *Diversity and Distributions* 14:234-242.

Gundale MJ, WM Jolly & TH Deluca. 2005. Susceptibility of a northern hardwood forest to exotic earthworm invasion. *Conservation Biology* 19:1075-1083.

Hedley J. 2004. The International Plant Protection Convention and invasives. Pages 185-201 in ML Miller & RN Fabian (eds) *Harmful invasive species: legal responses.* Environmental Law Institute, Washington DC.

IMO [International Maritime Agency]. 2004. *International Convention for the Control and Management of Ships' Ballast Water and Sediments*. Available at http://www.imo.org.

IPCC [Intergovernmental Panel on Climate Change]. 2007. *Climate change 2007: the physical science basis.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. Available at: www.ipcc.ch

ISSG [Invasive Species Specialist Group]. 2009. *Global invasive species database.* Available at: http://www.issg.org/database

IUCN [International Union for the Conservation of Nature]. 2000. *IUCN guidelines for the prevention of biodiversity loss caused by alien invasive species.* Available at: http://iucn.org.

Ivors K, M Garbelotto, IDE Vries, C Ryter-Spira, BTE Hekkert, N Rosenzweig & P Bonants. Microsatellite markers identify three lineages of Phytophthora ramorum in US nurseries, yet single lineages in US forest and European nursery populations. *Molecular Ecology* 15:1493-1505.

Jeschke JM & DL Strayer. 2005. Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences* 102:7198-7202.

Jones KE, NG Patel, MA Levy, A Storeygard, D Balk, JL Gittleman & P Daszak. 2008. Global trends in emerging infectious diseases. *Nature* 451:990-994.

Joshi R. 2005. Managing invasive alien mollusc species in rice. *International Rice Research Notes* 30:5-13.

Juliano SA & LP Lounibos. 2005. Ecology of invasive mosquitoes: effects on resident species and human health. *Ecology Letters* 8:558-574.

Keller RP & DM Lodge. 2007. Species invasions from commerce in live organisms: problems and possible solutions. *BioScience* 57:428-436.

Keller RP & JM Drake. 2009. Trait-based risk assessment for invasive species. Pages 44-62 in Keller RP, Lodge DM, Lewis MA and Shogren JF (eds) *Bioeconomics of Invasive Species*. Oxford University Press, New York.

Keller RP, DM Lodge & DC Finnoff. 2007. Risk assessment for invasive species produces net bioeconomic benefits. *Proceedings of the National Academy of Sciences* 104:203-207.

Keller RP, K Frang & DM Lodge. 2008. Preventing the spread of invasive species: economic benefits of intervention guided by ecological predictions. *Conservation Biology* 22:80-88.

Kilpatrick AM, AA Chmura, DW Gibbons, RC Fleischer, PP Marra & P Daszak. 2006. Predicting the global spread of H5N1 avian influenza. *Proceedings of the National Academy of Sciences* 103:19368-19373.

Knowler D, & E Barbier. 2005. Importing exotic plants and the risk of invasion: are market-based instruments adequate? *Ecological Economics* 52:341-354.

Kopp RE, FJ Simons, JX Mitrovica, AC Maloof & M Oppenheimer. 2009. Probabilistic assessment of sea level during the last interglacial stage. *Nature* 462:863-867.

Kumar L & R Hanna. 2009. *Tackling the banana menace. International Institute of Tropical Agriculture*. Available at: http://r4dreview.org/2009/03/tackling-the-banana-menace/. Accessed 29 December 2009.

Kutz FW, TG Wade & BB. Pagac. 2003. A geospatial study of the potential of two exotic species of mosquitoes to impact the epidemiology of West Nile virus in Maryland. *Journal of the American Mosquito Control Association* 19:190-198.

Lee J-W & WJ McKibbin. Estimating the global economic costs of SARS. Pages 92-109 in S Knobler, A Mahmoud, S Lemon, A Mack, L Sivitz & K Oberholtzer (eds) *Learning from SARS: preparing for the next disease outbreak.* The National Academies Press, Washington DC.

Leung B, DM Lodge, D Finnoff, JF Shogren, MA Lewis & G Lamberti. 2002. An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London Series B* 269:2407-2413.

Leung B, JM Bossenbroek, & DM Lodge. 2006. Boats, pathways and aquatic biological invasions: estimating dispersal potential with gravity models. *Biological Invasions* 8:241-254.

Leung B, JM Drake & DM Lodge. 2004. Predicting invasions: Propagule pressure and the gravity of allee effects. *Ecology* 85:1651-1660.

Levine JM, & CM D'Antonio. 2003. Forecasting biological invasions with increasing international trade. *Conservation Biology* 17:322-326.

Lockwood JL, P Cassey & TM Blackburn. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20:223-228.

Lodge DM, S Williams, HJ MacIsaac, KR Hayes, B Leung, S Reichard, RN Mack, PB Moyle, M Smith, DA Andow, JT Carlton & A McMichaell. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecological Applications* 16:2035-2054.

Loo SE, R Mac Nally, DJ O'Dowd & PS Lake. 2009. Secondary invasions: implications of riparian restoration for in-stream invasion by an aquatic grass. *Restoration Ecology 17:378-385.*

Low T. 2001. *Feral Future*. Penguin, Melbourne, Australia.

Mack RN, D Simberloff, WM Lonsdale, H Evans, M Clout & FA Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710.

Mahmoud AAF & AM Lemon. 2004. Summary and assessment. Pages 1-40 in S Knobler, A Mahmoud, S Lemon, A Mack, L Sivitz & K Oberholtzer (eds) *Learning from SARS: preparing for the next disease outbreak.* The National Academies Press, Washington DC.

Mangili A & MA Gendreau. 2005. Transmission of infectious diseases during commercial air travel. *The Lancet* 365:989-996.

Marais C & AM Wannenburgh. 2008. Restoration of water resources (natural capital) through the clearing of invasive alien plants from riparian areas in South Africa – costs and water benefits. *South African Journal of Botany* 74:526-537.

McMichael AJ & MJ Bouma. 2000. Global changes, invasive species, and human health. Pages 191-210 in HA Mooney & RJ Hobbs (eds) *Invasive species in a changing world.* Island Press, Washington DC.

MEA [Millennium Ecosystem Assessment]. 2003. *Ecosystems and human well-being: a framework for assessment.* Island Press, Washington, DC. Available at: http://www.millenniumassessment.org/

MEA [Millennium Ecosystem Assessment]. 2005. *Ecosystems and human wellbeing: general synthesis*. Island Press, Washington, DC. Available at: http://www.millenniumassessment.org/

MEA [Millennium Ecosystem Assessment]. 2005b. Food ecosystem services. Pages 209-241 in MEA *Current State and Trends*. Island Press, Washington, DC. Available at: http://www.millenniumassessment.org/

Mills EL, JH Leach, JT Carlton & CL Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19:1-54.

Mooney H, A Cropper & W Reid. 2005. Confronting the human dilemma. *Nature* 434:561-562.

Moyle PB & MP Marchetti. 2006. Predicting invasion success: freshwater fishes in California as a model. *BioScience* 56:515-524.

Naylor RN. 1996. Invasions in agriculture: assessing the cost of the golden apple snail in Asia. *Ambio* 25:443-448.

Oerke E-C. 2006. Crop losses to pests. *Journal of Agricultural Science* 144:31-43.

Oerke, E-C & H-W Dehne. 2004. Safeguarding production – losses in major crops and the role of crop protection. *Crop Protection* 23:275-285.

Paarlberg PL., Seitzinger AH, Lee JG and Matthews KH Jr. 2008. *Economic impacts of foreign animal disease*. United States Department of Agriculture, Economic Research Service, Report ERR-57.

Padilla DK & SL Williams. 2004. Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2:131-138.

Pejchar L & HA Mooney. 2009. Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution* 24:497-504.

Perrings C, K Dehnen-Schmutz, J Touza, & M Williamson. 2005. How to manage biological invasions under globalization. *Trends in Ecology and Evolution* 20:212-215.

Perrings C, M Williamson, EB Barbier, D Delfino, S Dalmazzone, J Shogren, P Simmons & A Watkinson. 2002. Biological invasion risks and the public good: an economic perspective. *Conservation Ecology* 6(1):1. Available at: http://www.consecol.org/vol6/iss1/art1.

Perrings C, S Burgiel, M Lonsdale, H Mooney & M Williamson. 2010. Globalization and bioinvasions: the international policy problem. Pages 235-249 in Perrings C., H. Mooney and M.Williamson. 2010. *Bioinvasions and Globalization: Ecology, Economics, Management and Policy,* Oxford University Press, Oxford, UK.

Perrings C. 2007. Pests, pathogens and poverty: biological invasions and agricultural dependence. Pages 133-165 in A Kontoleon, U Pascual & T Swanson (eds) *Biodiversity Economics: Principles, Methods and Applications*. Cambridge University Press, Cambridge, UK.

Peterson AT. 2003. Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology* 78:419-433.

Pheloung PC. 1995. *Determining the weed potential of new plant introductions to Australia* (Agriculture Protection Board, Perth, Australia).

Pimentel D (editor). 2002. *Biological invasions: economic and environmental costs of alien plant, animal, and microbe species.* CRC Press, Boca Raton, FL, USA.

Pimentel D, R Zuniga & D Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273-288.

Pinstrup-Andersen P. 2009. Food security: definition and measurement. *Food Security* 1:5-7.

Pounds JA, MR Bustamante, LA Coloma, JA Consuegra, MPL Fogden, PN Foster, E La Marca, KL Masters, A Merino-Viteri, R Puschendorf, SR Ron, GA Sanchez-Azofeifa, CJ Still & BE Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161-167.

Reed KD, JW Melski, MB Graham, RL Regnery, MJ Sotir, MV Wegner, JJ Kazmierczak, EJ Stratman, Y Li, JA Fairley, GR Swain, VA Olson, EK Sargent, SC Kehl, MA Frace, R Kline, SL Foldy, JP Davis & IK Damon. 2004. The detection of monkeypox in humans in the Western Hemisphere. *New England Journal of Medicine* 350:342-350.

Reichard SH & P White. 2001. Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience* 51:103-113.

Reiter P. 1998. Aedes albopictus and the world trade in used tires, 1988-1995: the shape of things to come? *Journal of the American Mosquito Control Association* 14:83-94.

Ricciardi A, RJ Neves & JB Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology* 67:613-619.

Ricciardi A. 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Diversity and Distributions* 12:425-433.

Rignot E. 2006. Changes in ice dynamics and mass balance of the Antarctic ice sheet. *Philosophical Transactions of the Royal Society a-Mathematical Physical and Engineering Sciences* 364:1637-1655.

Roberts J, A Chick, L Oswald & P Thompson. 1995. Effect of carp, Cyprinus carpio L., an exotic benthivorous fish, on aquatic plants and water quality in experimental ponds. *Marine and Freshwater Research* 46:1171-1180.

Rodda GH, CS Jarnevich & RN Reed. 2009. What parts of the US mainland are climatically suitable for invasive alien pythons spreading from Everglades National Park. *Biological Invasions* 11:241-252.

Roeder PL, J Lubroth & WP Taylor. 2004. Experience with eradicating rinderpest by vaccination. *Developments in Biologicals* 119: 73-91.

Romagosa CM, C Guyer & MC Wooten. 2009. Contribution of the live-vertebrate trade toward taxonomic homogenization. *Conservation Biology* 23:1001-1007.

Sala OE, FS Chapin, JJ Armesto, E Berlow, J Bloomfield, R Dirzo, E Huber-Sanwald, LF Huenneke, RB Jackson, A Kinzig, R Leemans, DM Lodge, HA Mooney, M Oesterheld, NL Poff, MT Sykes, BH Walker, M Walker & DH Wall. 2000. Global Biodiversity Scenarios for the Year 2100. *Science* 287:1770-1774.

Schneider L & Geoghegan J. 2006. Land abandonment in an agricultural frontier after a plant invasion: the case of bracken fern in Southern Yucatán, Mexico. *Agricultural and Resource Economics Review* 35:1-11.

Sheley RL, LL Larson & JS Jacobs. 1999. Yellow starthistle. Pages 408-416 in RL Sheley & JK Petroff (eds) *Biology and management of noxious rangeland weeds.* Oregon State University Press, Corvallis, OR.

Shogren JF. 2000. Risk reduction strategies against the 'explosive invader'. Pages 56-69 in C Perrings, M Williamson & S Dalmazzone (eds) *Economics of Invasive Species*. Edgar Allen, Northampton, MA, USA.

Sinden J, R Jones, S Hester, D Odom, C Kalisch, R James & O Cacho. 2004. *The economic impact of weeds in Australia.* CRC for Australian Weed Management, Adelaide.

Smith KF, MD Behrens, LM Max & P Daszak. 2008. US drowning in unidentified fishes: scope, implications, and regulation of live fish import. *Conservation Letters* 1:103-109.

Stohlgren TJ, DT Barnett & J Kartesz. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* 1:11-14.

Taylor LH, SM Latham & MEJ Woolhouse. 2001. Risk factors for human disease emergence. *Philosophical Transactions of the Royal Society of London Series* B 356:983-989.

Tchamba MN. 1996. History and present status of the human/elephant conflict in the Waza-Logone region, Cameroon, West Africa. *Biological Conservation* 75:35-41.

Thomas CD, A Cameron, RE Green, M Bakkenes, LJ Beaumont, YC Collingham, BFN Erasmus, MF de Siqueira, A Grainger, L Hannah, L Hughes, B Huntley, AS van Jaarsveld, GF Midgley, L Miles, MA Ortega-Huerta, AT Peterson, OL Phillips & SE Williams. 2004. Extinction risk from climate change. *Nature* 427:145-148.

Veltman CJ, S Nee & M Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. *American Naturalist* 147:542-557.

Versfeld DB, DC Le Maitre & RA Chapman. 1998. *Alien invading plants and water resources in South Africa: a preliminary assessment.* CSIR Division of Water, Environment and Forestry Technology, Stellenbosch, South Africa.

Vilà M & J Pujadas. 2001. Socio-economic parameters influencing plant invasions in Europe and North Africa. Pages 75-77 In J McNeely (ed.) *The great reshuffling: human dimensions of invasive alien species*. IUCN, Gland, Switzerland.

Virtue JG, SJ Bennett & RP Randall. 2004. Plant introductions in Australia: how can we resolve "weedy" conflicts of interest? Pages 42-48 in BM Sindel & SB Johnson (eds) *Proceedings of the 14th Australian Weeds Conference*. Weed Society of New South Wales, Sydney.

Vitousek PM, JD Aber, RW Howarth, GE Likens, PA Matson, DW Schindler, WH Schlesinger & DG Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* 7:737-750.

Weiss RA & AJ McMichael. 2004. Social and environmental risk factors in the emergence of infectious diseases. *Nature Medicine* 10:s70-s76.

Weyl OLF. 2008. Rapid invasion of a subtropical lake fishery in central Mozambique by Nile tilapia, Oreochromis niloticus (Pisces: Cichlidae). *Aquatic Conservation: Marine and Freshwater Ecosystems* 18:839-851.

Williamson MH. 1996. *Biological invasions.* Chapman & Hall, London.

Wilson ME. 1995. Travel and the emergence of infectious diseases. *Emerging Infectious Diseases* 1:39-46.