1. Introduction

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1 THE PROBLEM OF BIOLOGICAL INVASIONS

A large share of the attention attracted by biological invasions has been motivated, until recently, by the impact on crops of alien species that became pests. Living organisms have always been transported beyond their original range; however, because of the enormous growth in the international transport of people and commodities in the last quarter to half a century, invasions now have unprecedented environmental and economic effects.

In addition to their impact in terms of forgone output in agriculture, forestry and fisheries, pest control and health care, invasive species have proved to be one of the main drivers behind biodiversity loss in a wide range of ecosystems. The factors that have evolved with them and that control their population and spread in their native range are generally not present in their new habitats. Native species may not possess defence mechanisms that allow them to compete successfully for vital resources and may therefore be driven to extinction. Indeed, invasives are sometimes said to be the second most important cause of biodiversity loss, after habitat destruction (Glowka et al., 1994). They are certainly a major threat on oceanic islands. The extinctions due to cats, rats, goats, the snail *Euglandina rosea* and the brown tree snake *Boiga irregularis* are all well known (Williamson, 1996). On continents, the threat of invasives to biodiversity is variable. It is better known in developed countries than developing ones, but Mack (1997) notes invasives affecting whole landscapes in parts of the USA, Central America from Mexico to Panama, Venezuela, Brazil, Argentina, Iceland and many other smaller islands, South Africa, Madagascar, India, Myanmar, Australia and New Zealand, which is a mix of most types of economies. In the United States, invasives have been shown to be the major threat to imperilled species after habitat destruction (Wilcove et al., 1998). Czech and Krausman (1997), though, claimed that this is primarily an island effect; of 305 species endangered by non-natives, only 115 are on the mainland, but 190 are on Hawaii and Puerto Rico, both oceanic islands.

Many ecological functions are supported at any one moment in time by a relatively small number of species. Their removal can induce a transformation of the ecosystem (Holling, 1992; Heywood, 1995). The level of biodiversity in an agroecosystem determines its capacity to respond to external shocks, whether market or environmental. From an ecological perspective, biodiversity protects ecosystem resilience by underwriting the provision of ecosystem services over a range of environmental conditions (Holling et al., 1995). Certain species have greater ecological value under one state of nature than others, but species that are ‘passengers’ under one state of nature may have a key structuring role to play under other states of nature. The ecological impact of biodiversity loss depends on the link between the species and the functions of the system. Whether the deletion of some species affects a given function depends on the number of alternative species that can support the function if the ecosystem is perturbed (Schindler, 1990; Lawton and Brown, 1993). Invasive species may be critical in undermining the buffering role played by ecological redundancy.

Invasive species have a great variety of impacts, of which swamping of other species, diseases and new top trophic species (predators such as cats, herbivores such as goats) are generally the most severe (Williamson, 1996). Impacts have been measured in a great variety of different ecosystems, terrestrial, fresh-water and marine, animal, plant and microbe (Parker et al., 1999) and have a great variety of economic and ecological effects (Williamson, in press). Impacts vary more or less continuously from negligible to severe and each type of impact has its own spectrum of species, each species its own spectrum of impacts (Williamson, 1998). There is clearly a need for more modelling of impacts, and more experimental and observational research on the relation of different impacts and the ways of measuring them (Parker et al., 1999). Some of the remarkable variety of impacts are described, in a semi-scientific way, by Bright (1999) and Devine (1998) and the cases studies in this book, Chapters 5–11, give further instances.

With the growth of global economic activity, there will be many new impacts by invasives that will not be predicted (Williamson, 1999 and in press), but measures can be taken to avoid a repeat of old impacts in new areas, to forestall new impacts and to manage efficiently, both economically and ecologically, those species that cannot be eradicated. That is the contribution of this book to the Global Invasive Species Project.

2 THE GLOBAL INVASIVE SPECIES PROJECT

The chapters of this book are based on presentations at a symposium on the economics of invasive biological species held in York, England, in March

1999. The symposium was part of the Global Invasive Species Project, itself a programme of SCOPE, the Scientific Committee (of ICSU, the International Council for Science) on Problems of the Environment. GISP is funded from many sources but primarily by GEF, the Global Environment Facility of the United Nations. A major aim of the project is to improve implementation of Article 8(h) of the Convention on Biological Diversity which exhorts the Contracting Parties to 'prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species'. The Convention on Biological Diversity (CBD) was signed by more than 150 governments at the 1992 Earth Summit in Rio de Janeiro, and became effective as international law in December 1993. It is the first international agreement which commits governments to a comprehensive protection of the Earth's biological resources. As of November 1999, 176 countries have ratified the agreement.¹ At the core of the Convention is the recognition that diversity must be maintained, if only because failure to do so would threaten human existence. This is achievable only through sustainable use and a fair and equitable distribution of the benefits derived from the use. By signing the CBD, participating governments have agreed, among other things, to pursue policy measures such as creation of national plans for the protection of biodiversity, identification of ecosystems, species and genomes crucial for conservation, monitoring of biological diversity and of any factors that might have an impact on it, establishing systems of protected areas, rehabilitating damaged ecosystems, and taking measures for *ex-situ* conservation. The Convention comprises 42 articles concerning its objectives, the practical obligations of the signatories, the policies to be followed and the use of terms.²

GISP intends, *inter alia*, to provide advice about invasive species, and how to implement Article 8(h). Its audience includes decision makers responsible for health, agriculture, forestry, fisheries and the environment. That advice should include information on how to identify and estimate the economic effects of invasives, and on their prevention, control and mitigation. The symposium reported here is a first major step towards formulating and codifying such advice.

3 THE ECONOMICS OF INVASIVES

The core problems in the economics of invasives are, first, to understand the causes, consequences and economic forces behind invasions; and second, how to achieve an efficient allocation of resources to the prevention, control and mitigation of invasives, given socioeconomic and environmental conditions, and given the objectives of the decision makers.

Valuation is a part of this problem. Although economists recognize that the market prices of species and ecological services are poor indicators of their value to humanity, they have only recently begun to grapple with the problem of the valuation of biodiversity (Pearce and Moran, 1994). There is some consensus that the most appropriate methods for the valuation of non-marketed biological resources focus on their local opportunity cost – their impact on the range of services provided by the affected ecosystem (Heywood, 1995). To arrive at an appropriate valuation, therefore, requires an appropriate specification of the underlying physical problem and the attendant risks. It depends on getting the science of invasions right.

This requires that we are able to understand, measure, explain and predict invasions – a field recently reviewed by Williamson (1999). There are many biologists who would like to think that invasions can in principle be predicted, particularly from the general properties of species or habitats or both. The evidence, unfortunately, is that this is not and will not be possible. Part of the problem is that there seem to be no general laws governing biological invasions. Lawton (1999, p. 180) argues that ‘if we need, or want, to predict in detail the population dynamics of a particular species in a particular habitat, then there is no alternative but to study that species in detail in the place or habitat of interest’. Law et al. (in press) make a similar point: namely that understanding invasions depends as much on detailed knowledge of idiosyncratic biological interactions as on general properties of community structure. The advice of Kareiva et al. (1996) is that models and short-term experiments are inadequate predictors of invasions, so new situations will require extensive monitoring. In practice this means studying previous invasions by the same species. This approach was found by Williamson (1999) to be the only predictor other than propagule pressure that could be called ‘quite good’. Even though prediction is so difficult, explanations of the behaviour of invasives can be found by appropriate ecological studies (ibid.). That is sufficient to inform the economics of invasions. But the limitations of biological explanation and prediction need to be borne in mind when formulating economic protocols.

Whereas the management of pests in agriculture, forestry and fisheries has been extensively researched, there has been little systematic economic analysis of the broader problem of invasives. The economics of pest and disease control is the basis for most existing estimates of the cost of invasives. It is certainly the area in which data are most reliable. There are, for example, reasonably good estimates of the relative costs of herbicide control for different plant species in Britain (Williamson, 1998). There are estimates of the damages and/or the control costs also for a few other invaders. Bioeconomic or ecological-economic models have been employed to estimate the economic impact and the control costs of a potential invasion of Australia by the

Old World screwworm fly, *Chrysomya bezziana* (Anaman et al., 1994); the benefits from clearing alien species from Fynbos ecosystems in South Africa (Higgins et al., 1997b; Turpie and Heydenrych, Chapter 9, this volume); the impact of Knapweed and Leafy Spurge on the economy of several US states (Hirsch and Leitch, 1996; Bangsund et al., 1999); the damages to North American and European industrial plants from the zebra mussel and other invaders (Khalanski, 1997); the impact of the green crab *Carcinus maenas* on the North Pacific Ocean fisheries (Cohen et al., 1995); and the control costs for water hyacinth and rabbit, both discussed in chapters in this volume.

Many of these studies suffer from data limitations when dealing with the economic aspect of the problem, and most concentrate on estimates of costs and benefits, without developing decision models or theoretical analyses. Among the very few exceptions, Sharov and Liebhold (1998) and Sharov et al. (1998) develop an economic analysis of decisions about eradication, stopping, or slowing the spread of invasive species in North American ecosystems. They apply it to case studies of the gypsy moth *Lymantria dispar*. Higgins et al. (1997a) provide an ecological-economic model for the analysis of alternative strategies for control and conflict resolution in the case of environmental weeds whose eradication is resisted by parties who utilize them.

There are few attempts to aggregate the economic costs of invasions, and those that do exist vary very widely. Two estimates of the costs of invaders to the American economy, for example, are US OTA (1993) and Pimentel et al. (1999). The US OTA estimates damage costs of \$96 994 million from 79 particularly harmful species over 85 years. Pimentel et al. estimate damage costs of \$122 639 million per year from all species – a difference of two orders of magnitude (despite the apparent precision of both). Given this level of uncertainty about the severity of the problem, it is important to investigate the difficulties facing decision makers who deal with invasives, and how many resources should be committed to prevention, control and mitigation.

Part of the difficulty in producing estimates is that the aggregate cost of invasions is made up of innumerable components, most of which are subject to considerable errors of measurement that are compounded in the summation. In addition, none of the available estimates considers all the relevant components. One that is often neglected, for example, is the globally important loss of genetic information. There are few estimates of the magnitude of these costs but all indicate that the sums involved are not trivial (Heywood, 1995; Pearce and Moran, 1994). Most cultivated crop varieties and some livestock strains contain genetic material recently incorporated from related wild or weedy species, or from more primitive genetic stocks still used and maintained by traditional agricultural peoples. It has been estimated that at least half of the increase in agricultural productivity achieved in the last hundred years is attributable to artificial selection, recombination and

intraspecific gene transfer procedures (Perrings et al., 1995). The value of genetic diversity in this case lies in the fact that it provides the raw material for desirable genetic traits in crops. Genetic resources have been used to boost productivity of meat, milk and wool, impart resistance to pests, and help adapt animals to harsh environments. Traditional varieties are the result of millennia of selection by farmers, and are a major source of genetic diversity in agriculture and of genetic resources for plant breeding. 'Natural' habitats may contain wild populations of existing crops and these wild genepools are a valuable resource for crop improvement. Displacement of such genetic resources is a major cost of invasions in agroecosystems.

Aside from the direct costs of the prevention, control or mitigation, the economic cost of invasives also includes their indirect ecological consequences. Invasives may lead to changes in ecological services that are locally important, by disturbing the operation of the hydrological cycle including flood control and water supply, waste assimilation, recycling of nutrients, conservation and regeneration of soils, pollination of crops and so on (Daily, 1997). These services have both current-use value and option value – the potential value of such services in the future. As an example, an estimate of the indirect benefits of forest conservation in Korup National Park, Cameroon (Ruitenbeek, 1989) found the net benefits of watershed protection, flood control and soil fertility maintenance to be roughly comparable to the foregone benefits from timber production. A further example, described in this book, is the role of acacia species in the hydrological cycle in the South African Fynbos. A change in the biodiversity of the Fynbos induced by the establishment of an invasive species has changed water supplies to the whole community (Turpie and Heydenrych, Chapter 9, this volume). One aim of this book is to clarify how the direct and indirect costs of invasions may be assessed.

Agricultural pests, epidemic diseases, and the establishment of wild species in unmanaged ecosystems are all part of the same general problem. In many cases the introduction and establishment of new species is an external effect of market activities. Although the destruction of crops and harvests is usually reflected in the market prices of agricultural, fishery, or forestry commodities, these costs are not borne by the source of the introductions. They are in the nature of externalities – costs which a given activity unintentionally imposes on another, without the latter being able to exact a compensation for the damage received. The biodiversity loss caused by habitat destruction (but not that caused by poaching, for example) also falls in that general conceptual category.

There is, however, a notable difference between biological invasions and externalities as conventionally understood in economics. The generally accepted notion of external effect implies that, in order to persist, the damage

must be associated with a continuing flow of output from the source. Biological invasions, on the other hand, once set in motion are largely self-perpetuating. Even if the source of the introduction ceases its activity, damages from the invasives continue and generally increase over time. For this reason the policies developed to deal with conventional externalities and applied in the literature on general biodiversity loss – taxes and subsidies, the establishment of well-defined property rights, and possibly even permits and quotas – in all likelihood are ill-suited to deal with the problem of invasions. Consider, for example, the recent invasion of the North American Great Lakes by the fishhook waterflea (*Cercopagis pengoi*), expected to infest the entire ecosystem and to seriously disrupt sport and commercial fisheries (Mittelstaedt, 1999). Even if the cargo responsible for the introduction could be induced by an economic policy instrument to never return again to the region, the flow of damages would not be extinguished. Moreover, the identification of the pathways of introduction is a well-known problem among experts of invasions as well as policy makers – and so is the prediction of which species are a potential source of trouble. Indeed, the problems associated with uncertainty, monitoring and enforcement are all more severe than they are in the presence of conventional externalities.

4 THE STRUCTURE OF THE BOOK

The book is divided into two parts. The first part is concerned with the general theoretical and methodological issues raised by the problem of invasive species. The second part comprises case studies that collectively lead to important empirical generalizations about invasions. Both approaches are important and both will be needed to develop decision rules, tools and protocols for the effective management of invasive biological species. Chapter 12 offers some conclusions.

The evaluation of costs associated with invasive species and benefits of control strategies by no means exhausts the potential for an economic analysis of the problem of biological invasions. An economic approach can be aimed also at understanding mechanisms and relationships, at investigating causes and possible policies. It is important, for example, to identify the institutional and policy conditions that predispose countries to biological invasion. In the first part of this volume, the chapter by Dalmazzone (Chapter 2) is an initial step in that direction. Based on data concerning established alien plant species in 29 different countries in different continents, and a large number of economic variables – the composition of a country's trade flows, its regulatory regimes, the importance of agriculture, livestock, tourism sectors and so on – the chapter investigates the empirical support for the

hypothesis of economic activities as determinants in the recent changes in the rate of alien species introductions. The analysis constitutes a preliminary study of which economic activities are likely to play a role, and of their relative importance in explaining a country's susceptibility to biological invasions. It also aims at investigating the relative importance of disturbance (which may undermine the ability of ecosystems to resist to invasions) versus introductions of alien species as determinants of biological invasions.

From a different perspective, Delfino and Simmons (Chapter 3) regard infectious diseases as invasives into the human species and look at how the invasive disease interacts with the economy in which it occurs. Having outlined the invasive nature of the major infectious diseases, they look at the dynamic epidemiology of the human population. Then they explore how economically motivated mechanisms to control the disease affect the population dynamics. Finally they look at the main reasons for a regulatory control of human behaviours that may affect patterns of introduction and spread of the disease.

Shogren (Chapter 4) focuses on the risks that exotic invaders pose to both ecological and economic systems by disrupting traditional production systems. Societies reduce the risks posed by invaders through private and collective mitigation or adaptation or both. Mitigation reduces the odds that bad events happen; adaptation reduces the consequences when a bad event does occur. The chapter develops an analytical framework to capture how a society can mix mitigation and adaptation strategies to reduce the risk from exotic invaders. Using the economic theory of endogenous risk, three implications are considered – the interaction of biological and economic factors to assess risk, the value of risk reduction, and the impact of additional risk of damages.

The last two chapters in Part I apply models to particular case studies. Knowler and Barbier (Chapter 5) offer a conceptual framework for looking at the costs imposed by unintended species introductions. They develop a model of an introduction with consequences for an indigenous harvested species, whose population dynamics are altered by the invader. After discussing the general implications and costs associated with this event, they proceed to a case-study application of a particular variant of the model. The Black Sea offers one of the most interesting examples of a large commercial harvesting loss due mainly to an invading species – the comb-jelly *Mnemiopsis leidyi*, introduced in the early 1980s. The chapter contains a model of the population dynamics of the Black Sea anchovy, integrating the influence of the invasive as a structural change in the anchovy stock–recruitment relationship; it assesses the economic impact of this structural change using a dynamic discrete time bioeconomic model; and it provides estimates of the losses involved.

Annual weeds are present in all but the most intensively managed agricultural systems. In agricultural systems worldwide, many of these species are

not native but have invaded from elsewhere. Watkinson, Freckleton and Dowling (Chapter 6) outline how classical ecological models can be used to address some of the problems of invasive weeds, including (i) prediction of the numbers of weeds and the yield losses that result from their presence; (ii) the use of sensitivity analysis of population models in order to target key areas of the life cycle at which control will be most effective; and (iii) exploration of the general determinants of invasions. When information on the responses of populations to management and the cost of management are available, their approach feeds the predictions of ecological models into an economic analysis and predicts the optimum management strategies. These principles are illustrated with reviews of two case studies based on the invasion of Australian farming systems by weeds from Europe.

The chapters in Part II focus on five representative case studies. White and Newton-Cross (Chapter 7) focus on rabbits – Australia's most serious vertebrate pest. Rabbit grazing causes considerable economic damage to agriculture and forestry and also has adverse effects on the native flora and fauna. Their chapter assesses the market and non-market values associated with the introduction of rabbit calicivirus disease (RCD), officially released throughout Australia in October 1996, as a biological control agent for rabbits. The market values include costs and benefits accruing to the public sector, agriculture, forestry, the commercial rabbit industry and pet owners. The non-market values include costs and benefits to the wider ecosystem including native fauna and flora. Based on current scientific knowledge, the benefits of the introduction of RCD appear to exceed the costs considerably. However, some uncertainty remains about key aspects such as the long-term stability of RCD itself.

The impact of invasive plant species in tropical rain forests is a much debated issue. Lovett (Chapter 8) argues that, in that domain, concerns over the impact of invasive species are often not articulated within an ecological or a financial economic reasoning. Rather they are the result of a perceived change in the rain forest from an undisturbed *Urwald*, to a derived secondary type of forest. Lovett sees the arrival of new species in ecosystems as a normal process that has led to the accumulation of biological diversity. The main reason for concern is then perceived in terms of existence values or citizens' preferences for a particular state of nature. This point of view is illustrated using the case of *Maesopsis eminii*, a tree considered as an invasive in the Eastern Arc rain forests of Tanzania, an area listed as one of the Earth's most important biodiversity hotspots.

The South African Cape Floral Kingdom, with its characteristic Fynbos vegetation, is the smallest but richest of the world's six floral kingdoms. While facing a number of threats, its integrity is most severely threatened by the invasion of alien plants which rapidly transform natural areas into

monospecific stands. These invasions, which already affect 66 per cent of the remaining Fynbos area in the Western Cape, not only reduce biodiversity and scenic beauty, but alter ecosystem functioning. Turpie and Heydenrych (Chapter 9) argue that Fynbos mountain catchments are extremely valuable in terms of their water yield, and this service is reduced significantly by alien invasions. While there has been some previous research on Fynbos's contribution to the hydrological cycle, this study also provides estimates of the value it yields in the form of consumptive use benefits, non-consumptive use value and option and existence values. The incentives to clear invasive aliens are evaluated depending on location (mountain ecosystems, agricultural land and so on) and property right regime (protected areas, private property, public property). The chapter reviews also the internationally funded Working for Water Project, initiated by the South African government in 1995 as a result of research which demonstrated the water benefits of alien eradication. That project has also turned alien clearing into a source of poverty relief through the creation of jobs, in addition to its value in terms of biodiversity conservation.

Kasulo (Chapter 10) analyses the ecological and socioeconomic impact of invasive species in African lakes. The focus is on introduced fish species and water weeds – in particular, the chapter analyses the biological and economic implications of the introduction of Nile perch, the Tanganyika sardine, and water hyacinth into Lakes Victoria, Kyoga, Nabugabo, Kariba, Kiw, Itezhi-tezhi and Malawi. The introduction of Nile perch has increased profits from commercial fishing and contributed to the generation of foreign exchange. However, the Nile perch is believed to have caused the extinction of numerous endemic species. The introduction of the sardine also resulted in an increase in productivity, with less dramatic impact on the lakes' ecosystem. The water hyacinth, introduced in Africa as an ornamental plant, has proliferated explosively in most African lakes, obstructing water passages and displacing native aquatic plants, fish and invertebrates by cutting out light and depleting dissolved oxygen. The weed is also believed to harbour disease-carrying organisms, and has little potential for economic utilization.

In Chapter 11, Hill and Greathead are concerned with biological control as a tool to counteract invasions. Approximately 10–15 per cent of some five thousand classical biological control introductions against arthropods have proved completely successful. Against weeds, about 30–40 per cent of some nine hundred introductions have achieved their objective. While most attempts at classical biological control are failures, a review of 27 economic analyses of successful programmes shows that they are extremely profitable, so much so that the successes may comfortably cover the costs of the failures. Research and fund managers need better tools to assist them in increasing the ratio of successes to failures, thereby increasing further the return on invest-

ment in biological control. In this regard, decision support tools incorporating economic and technical parameters are needed for *ex-ante* analyses to help assess the economic and non-economic impact of invading species and the probability of successful biological control.

We are a long way from a comprehensive and consistent economic theory of biological invasions. Whereas invasive species are attracting increasing scientific attention as many countries' budgets for control measures are on the rise, the economics of the problem has so far attracted little attention. The chapters in this volume represent a first coordinated attempt in that direction, provide a few of the essential building blocks, and – we hope – improve our understanding of the economic mechanisms behind biological invasions relative to what it was before.

NOTES

1. The Convention has not been ratified by Afghanistan, Azerbaijan, Kuwait, Liberia, Malta, Thailand, the United Arab Emirates, the United States of America and the Federal Republic of Yugoslavia.
2. For a comprehensive guide to the CBD, see Glowka et al. (1994). A concise account is, for example, Gaston and Spicer (1998, pp. 94–105).

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