Bioeconomics of Invasive Species

Integrating Ecology, Economics, Policy, and Management

Edited by
Reuben P. Keller
David M. Lodge
Mark A. Lewis
Jason F. Shogren

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Foreword

This is a book that all ecologists and economists interested in bioeconomics should read. The master narrative encompassing a bi-disciplinary framework and endogenous risk makes it intuitively and logically appealing. A narrative that can be generalized in such a straightforward manner constitutes a forceful principle for organizing research and for informing policy. The work here should leave even the disciplinary isolationist interested in studying more about what a joint determination framework can offer.

Invasive species are a major environmental policy challenge. They continue to alter, often in undesirable ways, the workings of ecosystems around the globe. This book provides general and species-specific overviews of ecological and economic tools and also consensus propositions for studying interactions of the determinants and behaviors of invasive species. It treats lessons from past attempts to understand and to manage invasive species. It also suggests strategies for understanding and combating the threats to environmental and economic well-being that nonindigenous species pose. Readers will get a thorough treatment of the relevant scientific issues as well as a comprehensive review of the analytical and the empirical tools used by ecologists and economists to research invasive aquatic and terrestrial flora and fauna in North America and around the world.

Pleas for collaboration between ecologists and economists to advance understanding and resolution of environmental problems are so commonplace as to be almost hackneyed. When adherents of each disciplinary personality try to work together, they usually lapse into discord, followed by retreat into remote if not totally separated intellectual pursuits. Most ecologists and economists see only dimly how to clarify assumptions about their respective disciplines. The book provides a master narrative in which ecological and economic expertise complement and make each area more robust than were it to stand alone.

Ecological and economic systems each mediate the behaviors of the opposite system. The appropriate focus is the decision maker working in her or his environment, for in reality, neat separation of natural and human activities does not exist. A species' initial invasion, establishment, spatial spread, and temporal persistence influences and is influenced by abiotic and biotic processes and by individual and institutionalized human decisions. Decision makers adapt to environmental change by changing their personal behaviors as well as by directly changing a particular environment. Interactions and feedback between and among systems and system scales influence the structure, resilience, and dynamics of respective systems. Thus, jointly determined vision encourages individuals from each discipline to consider and understand what the other brings to the table. Each discipline is thereby forced to better scrutinize and document the information needs of the other. Such a vision supplies a framework for fostering sharper questions as well as sharper and smarter answers. This volume makes better-informed outcomes possible.

The focus of this book is on the bioeconomic behavioral roots of invasive species. Evaluation techniques (e.g., energy analysis, benefit–cost analysis) take a secondary role. The authors primarily address what does happen rather than what should happen. They present empirical illustrations demonstrating that the joint determination vision produces different answers from those arising from a framework based solely on either the ecological or the economic system.

Framing the causal relations between the ecology and the economics of invasive species as reciprocating systems does not imply that researchers should reform their entire set of ecological and economic tools or the tenets these tools have uncovered. Similar tools will likely be employed to develop propositions and to extract empirical results, whatever framework is used.

It is possible for model components to become so entangled in a web of interconnectedness, especially when some components are ill defined, that explanatory power is lost rather than gained. Parsimony can trump completeness, implying that there has to be some limit to the reciprocal coupling of the ecological and the economic components of an environmental model. Some intellectual separation is necessary to mark distinctions in system integration and to assure empirical content. This book acknowledges the parsimony–completeness tradeoff. Given limited research budgets and policy goals, this tradeoff immediately brings up the question of those facets of an invasive species model for which accuracy (unbiasedness) and precision (low variability across independent measurements) are especially important. Though the authors offer no firm answers to this question, the background they provide on invasive species will help formulate answers. A key extension of joint determination runs throughout the book. Uncertainty, irreversibilities, and timing issues almost always characterize invasive species problems. Uncertainty about causes or consequences shifts the focus to endogenous risk, a scenario in which decision makers can try to alter the risks (the product of probability and severity, if realized) of the establishment, spread, and persistence of an invasive species. An endogenous-risk focus has the potential to make less costly the tradeoff between model parsimony and completeness. A careful reading of this book strongly conveys this impression.

Whatever the issue, complexity and ambiguity tempt policy makers and even scientific experts to wrap themselves in a cloak of objectivity by picking and choosing the scientific results they deem relevant. The authors are alert to this temptation. Policy makers and experts must often transfer findings from existing original studies to new areas of scientific or policy interest. Several chapters here consider the transfer question. They ponder both the theoretical underpinnings of the question and its statistical and computational treatment. In particular, the authors recognize that combining information from multiple sources and models of a common phenomenon can produce parameter estimates corresponding more closely to a new setting than can any single source.

The book concludes with an appealing human touch. The editors recall and reflect upon the successes and failures of their research and their attempts to communicate and to convince the public and policy makers about the causes and likely consequences of invasive species problems. They view their records of success as mixed. This tentativeness is leavened by the cheery optimism of a young ecologist recounting what inspires him about invasive species research. He nevertheless expresses bewilderment at the frequent reluctance of policy makers and the public to learn about and to accept scientific results.

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Preface

Biological invasions can drive global environmental change. Biologists have explained the risks so that both the public and policy makers are now aware of the impacts of invasive species. Economists are also taking greater interest in determining how invasive species interact with economic systems, and in how invaders should be controlled to increase societal welfare. Disciplinary work by ecologists and economists expands our understanding of the drivers and impacts of invasions, but neither ecological nor economic systems operate in isolation. This book provides a greater integration and synthesis of ecological and economic concepts and tools—a bioeconomic approach to understanding and managing invasive species. Such an approach can help policy makers and the public determine optimal expenditures, for example, on preventing and controlling invasive species.

The Integrated Systems for Invasive Species (ISIS) team is a multi-institution collaboration among ecologists, economists, and mathematical biologists. The team came together as a project funded by the U.S. National Science Foundation and has met annually since 2000 (and conducted much research between meetings) to identify and address key questions about the bioeconomics of invasive species. The questions and our best responses are presented here. Our framework blends the work of the ISIS project with results from other researchers working on both disciplinary and interdisciplinary frontiers. Our group's composition ensures analytical and empirical rigor, as well as ecological and economic realism.

As society becomes more aware of global environmental change, people are demanding that policy makers address broader biological and economic realities. This book has two related goals. The first is to reinforce the role of bioeconomic research as the best approach to design policy and management systems for invasive species. The second is to show how bioeconomic research can be conducted to generate realistic invasive species policy recommendations. Throughout the ISIS project, we aim to place our bioeconomic research approach into a context that is useful to researchers and society.

The book's structure follows the linked economic and ecological processes that lead to invasion—starting with the vector of introduction, through establishment and spread, to the impacts of successful invaders. Our main thesis throughout is that a bioeconomic approach is required both to understand and to manage invasions. The first two chapters introduce the study of species invasions and give the rationale for this thesis. The next four chapters track the invasion process, including risk assessment tools to predict the identity of likely invaders and methods to identify the extent of suitable habitat for non-native species, also treating model approaches for predicting species establishment and dispersal. We consider throughout how the science can inform management and policy actions to reduce total impacts. Next we explore general issues, addressing uncertainty in models and methods for economic valuation, then tie it all together in an integrated bioeconomic model for determining appropriate management decisions in response to particular species invasions. The final four chapters include case studies based on ISIS research and a discussion of the possibilities and challenges for future bioeconomic research.

We gratefully acknowledge the funding agencies that have supported the ISIS project. These include the U.S. National Science Foundation, the Economic Research Service of the U.S. Department of Agriculture, the U.S. Environmental Protection Agency, the U.S. National Oceanographic and Atmospheric Agency (both directly and through SeaGrant), and the Natural Sciences and Engineering Research Council of Canada. We thank the Banff International Research Station for providing us a retreat where we edited the book.

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Introduction to Biological Invasions: Biological, Economic, and Social Perspectives

David M. Lodge, Mark A. Lewis, Jason F. Shogren, and Reuben P. Keller

In a Clamshell

Invasive species are now recognized worldwide as a serious side effect of international trade. They often spread irreversibly, and damages increase over time. To reduce such damages, private and public investments are increasing in an effort to prevent the arrival of species or eradicate them early in an invasion, control their local abundance once they have become established, or slow their spread. Most often, however, the damages of invasive species are accepted as a new cost of doing business, and humans change their behavior to minimize the impact. In this chapter, we argue that integrating ecological and economic analyses is essential to guide policy development in support of more cost-effective management. A key goal is to describe quantitatively the feedbacks between economic and ecological systems and to provide answers to such questions as how many dollars should be invested in prevention versus control, and what benefits are derived from such investments. This chapter describes the impacts of some high-profile invasive species, explains the extent to which ecological and economic systems are integrated, and looks to epidemiology for a model of how research and management could be better integrated to inform policy.

In the last two decades, experts and the public have recognized two important things about many anthropogenic environmental changes: first, these changes are increasingly global in scope, and second, they are hard to reverse. These characteristics apply with special force to harmful nonindigenous species, which we refer to as "invasive species" throughout this book. Both the global scope and the difficulty of reversing invasions impart considerable urgency to increasing our understanding of this problem. Invading organisms reproduce and spread, even if we cease introducing more individuals. The problem of harmful invasive species gets worse without management.

Research to better understand invasions comes naturally to scientists and social scientists, especially to those of us in universities. We also, however, believe it is urgent to focus our research on questions important to natural resource managers and policy makers, given society's explicit desire to reduce the current and future damages caused by invasive species. We want our research and its implementation to increase social welfare. Using the perspectives and tools of economists is appropriate because invasive species are, by definition, driven by human activities, usually commercial enterprises. Solutions will derive from changes in industry practices and consumer behavior.

Humans are as much the target of our study as the species that humans move around the globe. If research is to inform natural resource management and policy, it must be conducted collaboratively by natural and social scientists, and in the context of possible management and policy responses to invasive species. We elaborate on these general points after considering some specific examples of invasive species, their environmental and economic costs, and societal responses to them.

CAULERPA: SUCCESSFUL ERADICATION

Aquarium keepers, like owners of all sorts of plants and animals, sometimes tire of the organisms under their care and release them. In 2000, populations of the invasive seaweed *Caulerpa taxifolia* were discovered in two Southern California coastal embayments. This species, including a very invasive strain, has been sold widely in aquarium shops because it is fast growing, hardy, and beautiful (Walters et al. 2006). Some of these same characteristics have caused a well-documented history of harmful invasions. In various invaded marine ecosystems, including the Mediterranean Sea, commercial and recreational fishing, recreational activities like scuba diving, and tourism have all suffered (Meinesz 1999). When the species was discovered in California, a consortium of private and government agencies launched a concerted eradication effort using chlorine applications under anchored tarps. The effort cost at least $3.7 million over 5 years (Woodfield and Merkel 2005), and it was successful.

Without policy responses to prevent additional *Caulerpa* introductions, however, the need for many similarly expensive management situations would probably occur in the future as other naive aquarium owners dispose of unwanted plants (Walters et al. 2006). The U.S. Department of Agriculture (USDA) used its authority under the Plant Protection Act of 2000 to declare the Mediterranean aquarium strain of *C. taxifolia* a federal noxious weed. Such a designation gives the USDA authority to prohibit importation, exportation, or movement of the species in interstate commerce. In 2001, the state of California went a step further and made it illegal to possess *C. taxifolia* and nine other *Caulerpa* species. Nevertheless, various species and strains of *Caulerpa* remain easy to purchase in all states (Walters et al. 2006). The story of *Caulerpa* eradication near San Diego, then, is a success story. It is an example of successful implementation of a strategy referred to as "early detection, rapid response, and eradication," supported by additional efforts (of minimal success thus far) to prohibit future introductions.

SEA LAMPREY: SUCCESSFUL CONTROL

Across the continent and about a century earlier, the construction of the Welland Canal by-passed Niagara Falls and allowed sea lamprey (*Petromyzon marina*), along with ships and barges, access to the upper Great Lakes. Despite the fact that most sea lamprey previously lived their adult lives in the Atlantic Ocean, large and self-sustaining populations soon thrived in the upper lakes. While the increased navigation fostered commercial activities that were beneficial to humans, the invasion by sea lamprey was not. Adult sea lamprey are parasitic on other fish species, using their rasping and suckerlike mouth to feast on the blood of commercially valuable species such as lake trout (*Salvelinus namaycush*) and whitefish (*Coregonus* spp.). The result was declining fisheries and a public outcry.

Fortunately, larval sea lamprey are confined to the tributaries of the Great Lakes, where they reside for about 7 years before assuming their adult bloodsucking habits. The larvae are easy to locate and are highly susceptible to TFM (3-trifluoromethyl-4-nitrophenol), a chemical discovered in 1955. When applied at appropriate concentrations in tributaries, TFM kills sea lamprey larvae with acceptably low effects on other species. Since 1956 the United States and Canada have together spent about $15 million annually on monitoring and poisoning sea lamprey. Sea lamprey populations plummeted, and harm to the fisheries is kept tolerably low with these continuous expenditures. The management efforts directed at sea lamprey constitute a remarkably successful "control" effort, the ongoing expense of which is justified by even larger benefits in the protection of Great Lakes fisheries.

GYPSY MOTH: SUCCESSFULLY SLOWING THE SPREAD

In 1869, gypsy moth (*Lymantria dispar*), which had been imported from its native range in Europe, escaped an unsuccessful attempt at silk production in Massachusetts. Thus began an invasion of North America that is ongoing today. Gypsy moth infestations can completely defoliate vast forests of oak and other trees and can achieve such abundance that their excrement and bodies are sometimes a serious nuisance in urban areas. Outbreaks of gypsy moths are often controlled with an aggressive integrated pest management program. In areas where the gypsy moth is now a permanent resident, expenditures to keep their populations acceptably low are very high when the periodic population outbreaks are treated with pesticides. As for sea lamprey, the best that can be hoped for in these areas is successful control, not eradication. Therefore, for every acre that becomes infested as the invasion progresses, future control costs will be high (perhaps forever) if pesticide treatments are chosen. Otherwise, humans must simply adapt (*sensu* economics, not evolution) to the periodic damage to urban and natural forests.

Because of the damage and/or control costs once gypsy moths become established, the USDA and states from Wisconsin south to North Carolina spend about $12 million annually to slow the southwestward march of gypsy moths across the country. A combination of trapping, aerial spraying of insecticides, and mating-disrupting pheromones has slowed by 50% the advance of the invasion front, from about 13 miles per year to about 6 miles per year (Sharov et al. 2002). Although this effort is expensive, it is cost-effective because damages are avoided, at least for a year, in the area in advance of the invasion front—an area of roughly 9,000 square miles (1,500 miles × 6 miles). The avoided damages are much higher than the costs of the slow-the-spread program (Sharov 2004). Preventing long-distance, especially human-mediated, dispersal ahead of the advancing invasion front remains a challenge for this program, but overall the scientific and management responses to the gypsy moth are a successful example of a slow-the-spread strategy.

MOST OTHER INVASIVE SPECIES: UNCONTROLLED DAMAGES AND UNCHECKED SPREAD

Stories that end in at least some level of success—eradication of *Caulerpa*, control of sea lamprey, slowing the spread of the gypsy moth—are rare and unfortunately are vastly outnumbered by harmful invasions that proceed apace to a grim and often irreversible outcome. Some of the most visible, dramatic, and widespread examples come from forests.

In the United States, a combination of nonindigenous insects, fungi, and other parasites and pathogens have essentially extirpated American chestnut (*Castanea dentata*) and American elm (*Ulmus americana*), previously two of the dominant trees in eastern natural and urban forests, respectively (Burnham 1988; Gilbert 2002). Many other beloved and valuable species seem likely to face a similar demise from ongoing invasions: flowering dogwood (*Cornus florida*), destroyed by the anthracnose pathogen, has declined in abundance by more than 90% in some forest types over the last two decades (Holzmueller et al. 2006); American beech (*Fagus grandifolia*) is succumbing to beech bark blister; Eastern hemlock (*Tsuga canadensis*) is declining as the hemlock wooly adelgid spreads across the East and Midwest; butternut (*Juglans cinerea*) invariably dies after infection by butternut canker, which is common and spreading in the Northeast and Midwest (Ostry and Woeste 2004); mortality of ashes (*Fraxinus* spp.) hovers near 100% as the emerald ash borer advances across the Midwest (BenDor et al. 2006); and several species of oak (*Quercus* spp.) are vulnerable to sudden oak death, the spread of which has only recently begun but has already jumped from the West Coast to the East Coast in the nursery trade (Gilbert 2002). All the responsible pests and pathogens are nonindigenous, with many arriving in the United States as hitchhikers in shipments of plants, wood products, or wood packing material.

It is not just accidentally introduced pests and pathogens that damage forestry production and damage natural and urban forests. Deliberately introduced plants, such as the kudzu vine (*Pueraria lobata*), are also outcompeting native vegetation for light, nutrients, and space. And, like the gypsy moth, they can seem like a good thing at first. The American public first saw the fast-growing, attractively purple-flowered kudzu vine from Japan at the 1876 Centennial Exposition in Philadelphia (Forseth and Innis 2004). For decades thereafter, particularly in the southeastern United States, it served well as an ornamental plant that also provided summer shade under overgrown porches. Later, especially during the first half of the twentieth century, as justifiable concerns grew about the severe soil erosion and nutrient depletion that accompanied intensive cotton agriculture, the U.S. government distributed 85 million seedlings, paying southern farmers to plant them (Forseth and Innes 2004). As for so many introduced species, only later did the downsides to kudzu become apparent, especially as other economic forces caused the decline of row cropping and livestock operations that had included management of kudzu. Millions of kudzu plants began to escape control altogether (Forseth and Innes 2004).

By mid-century, the costs of kudzu had become painfully obvious. Kudzu now occurs from Texas to Florida and north to New York, covering over 3 million hectares, which increases by about 50,000 hectares per year (Forseth and Innes 2004). Forest productivity losses are between $100 million and $500 million per year, power companies spend about $1.5 million annually to control kudzu, and a 6-year effort was required to eradicate kudzu from the Chickamauga and Chattanooga National Military Park. The best that can be hoped for is locally successful eradication efforts, whose long-term success depends on continued monitoring and control, as the species continues to expand its geographic range from the southeastern United States. Unfortunately, the list of deliberately introduced plants like kudzu that have become very harmful to agriculture, livestock, forestry, and natural ecosystems is long, including hundreds of species. It also continues to grow.

In addition to lost productivity and increased expenditures for control efforts in human-managed landscapes, the result of these invasive species is an ongoing shift in the composition of forests that is similar in magnitude to that of a nationwide forest fire, only slower. Large negative consequences exist for industries involving horticulture, landscaping, wood products, recreation, and tourism, as well as for natural ecosystems. Forest ecosystems provide the most obvious examples of damaging, unreversed invasions, but the same patterns characterize other terrestrial, marine, and freshwater ecosystems.

Zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. bugensis* (= *D. rostriformis bugensis* [Andrusov (1897)])) are the best-documented examples of similar phenomena in freshwater ecosystems in North America. Both are small striped bivalve mollusks. Zebra mussel was discovered in Lake St. Clair, between lakes Erie and Huron, in the mid-1980s, with quagga mussels following within a few years. These mussels were released when ships discharged ballast water that had been taken up in a port in northern Europe, where zebra and quagga mussels had previously invaded from their native ranges around the Black Sea. With those ballast water releases, Lake St. Clair, and quickly other Great Lakes, became the beachhead for ongoing invasions of freshwater ecosystems of North America. From the Great Lakes, two major human-driven vectors of dispersal allowed zebra and quagga mussels to spread. First, the Chicago Sanitary and Ship Canal provided a ready conduit for the mussels to escape Lake Michigan (crossing a former watershed divide) and colonize the Illinois and Mississippi rivers downstream. From the Mississippi River proper, the mussels, especially zebra mussel so far, hitched rides upstream on barges to colonize tributaries, including the Ohio, Tennessee, and Missouri rivers.

Second, recreational boaters, who often visit multiple rivers and lakes, inadvertently carried mussels overland on their boat trailers and boats to inland lakes that are not connected by water to initial sites of infestation. Within a decade, zebra mussel colonized much of the Great Lakes–St. Lawrence River and Mississippi River drainage basins. In 2007 and 2008, colonization of the West Coast by quagga and zebra mussels, respectively, began. Quagga mussel was discovered in Lake Mead, the Colorado River, and the California Aqueduct (Stokstad 2007), while zebra mussel was discovered in a California reservoir. Much suitable habitat for zebra and quagga mussels remains to be colonized east of the Appalachians and in the West, including the Columbia and Sacramento-San Joaquin rivers (Drake and Bossenbroek 2004). While the probability of transport of live mussels to those regions from the Midwest is lower than to waterways in the Midwest, mussels are being transported, and without increased slow-the-spread efforts, these regions almost surely will be colonized and suffer damages in the future (Bossenbroek et al. 2007), especially with new sources of invasion in the western waterways.

Efforts to slow the spread of mussels are occurring at regional, state, and federal levels, but their efficacy is poorly documented, and they are almost certainly underfunded (Leung et al. 2002; Lodge et al. 2006). Additional investments in such efforts are warranted because the damages caused by zebra mussels are large, including at least $150 million annually in the Great Lakes region by clogging up water intake pipes in power plants, municipal water supplies, and industrial facilities that withdraw raw surface water (O'Neill 1996). In addition, sharp zebra mussel shells foul beaches, hinder recreation, extirpate native clam species, increase harmful algal blooms, and likely contribute to botulism outbreaks that devastate migrating waterfowl and fishes in the Great Lakes region (Yule et al. 2006). Zebra mussels are successfully (if expensively) controlled inside industrial facilities, and have been eradicated from one quarry lake in Virginia, but no technique exists to reduce the population of zebra mussel in an entire lake or waterway without killing many other organisms.

The zebra mussel invasion, like those described above for terrestrial ecosystems, will continue, more slowly perhaps if a more effective slow-the-spread campaign is implemented, but humans in North America are stuck with zebra and quagga mussels. Forevermore in North America, they will be abundant, and native clams and many other native species will be less abundant, some perhaps extinct (Strayer and Malcom 2007). The changes in our behavior to cope with these changes, and the expenditures necessary to control them in power plants, will likely grow over time until zebra and quagga mussels occupy all suitable waterways in North America. And many other invasive species already in the Great Lakes are following the mussels across the country.

The invasive species vignettes above bring up a very important question: is prevention a management option? Though prevention is little practiced in North America, the answer is yes, of course, prevention is possible. Slow-the-spread programs show that, on a regional scale, prevention is possible even if only temporary. Prevention is also possible at the continent's borders. Anyone who has returned to North America from a trip abroad knows not to try to bring any fresh fruit, or the insects or pathogens that it might harbor, into the country. And some rare rigorous inspection programs at borders show how much potential damage could be avoided with rigorous screening and interdiction programs. For example, comprehensive inspections of air cargo at Kahului Airport, Hawaii, during 20 weeks in 2000–2001 revealed 279 insect species, 125 of which were not known from Hawaii, and 47 plant pathogen species, 16 of which were not known from Hawaii (Hawaii Department of Agriculture 2002). Most of the time at this and other airports in North America, however, inspections are far fewer. Such organisms ordinarily go undetected and are released into the environment. Some will cause great harm.

Prevention is possible, then, but it is reasonable to wonder how much prevention would cost, and whether it would be cheaper than the damages that occur in the absence of prevention. The vignettes above illustrate how costly invasions can be, either through damages suffered or the expenditures to support eradication or control efforts, but would prevention be equally costly? These sorts of questions motivate much of this book. Despite the slowness of these and many other unfolding invasion disasters, they should be regarded with urgency because the costs are high, grow over time as the populations of harmful species spread, and are too often irreversible. Are we simply stuck with such costs, or are prevention and more aggressive control approaches viable alternatives? In this book, we focus on freshwater examples to illustrate the causes, consequences, and potential management responses to invasive species. We combine ecological modeling with economic modeling to answer questions about management and policy.

HUMAN VALUES

Human values determine both which environmental changes we call damages and what investments in management responses seem appropriate. The positive and negative values that humans assign to species or other characteristics of ecosystems are appropriately informed by various financial, scientific, religious, and ethical considerations, but inescapably it is humans that do the valuing and responding (Hamlin and Lodge 2006). Invasions occurred before humans appeared, but the rate at which global commerce now causes them is orders of magnitude higher than natural background rates (Lodge and Shrader-Frechette 2003). More and increasingly international transportation of goods causes invasions, and human behavior will either continue to increase invasions or rein them in. The combination of natural and social science represented in this book is essential to both diagnose invasions and respond to them.

Invasion Process and Feedbacks between Biological and Economic Systems

Following the vignettes above, we could continue to illustrate the issue of invasive species with thousands of additional examples, replete with idiosyncratic biological details. Such catalogs of examples, however, can obscure the processes that are common to all invasions (figure 1.1, left column). Understanding the processes, in turn, is essential to prescribing appropriate management responses (figure 1.1, right column).

Species are carried in a vector, which transports the species either overtly (e.g., the pet and horticultural trades) or incidentally (e.g., insect pests in lumber shipments, ballast water of ships, viruses carried by humans themselves) (figure 1.2). Depending on the traits of the species, and the conditions and the duration in the vector, some proportion of the organisms may be alive when they are released or escape at a location outside their native range.

Depending on the taxonomic group of organisms, many to most species subsequently go extinct in a new location, but a proportion—on the order of 5% for plants (Keller et al. 2007) and up to 50% for animals (Jeschke and Strayer 2005)— establish a self-sustaining population. While some of these established species remain localized, perhaps not even detected by humans, a proportion, again about 5–50%, spread

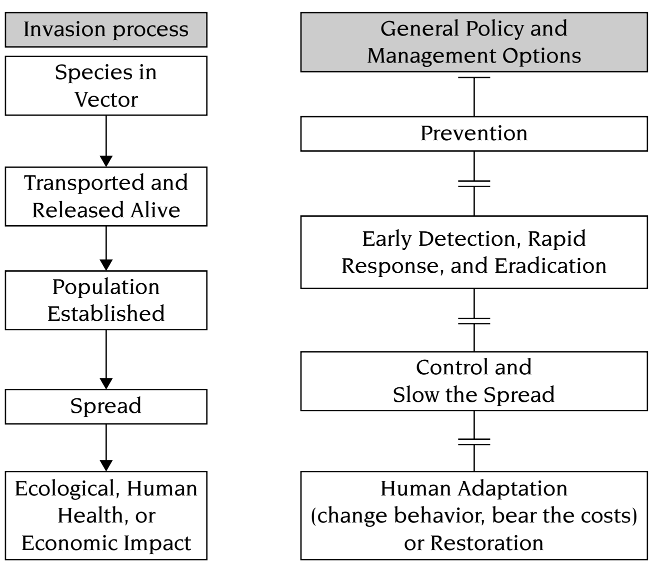

FIGURE 1.1.
The stages of biological invasion (left column) and the management and policy options available to society (right column) at each stage of invasion. The desire to reduce the negative impacts of species (bottom left) motivates the study of biological invasions. Reprinted from Lodge et al. (2006), with permission of the Ecological Society of America.

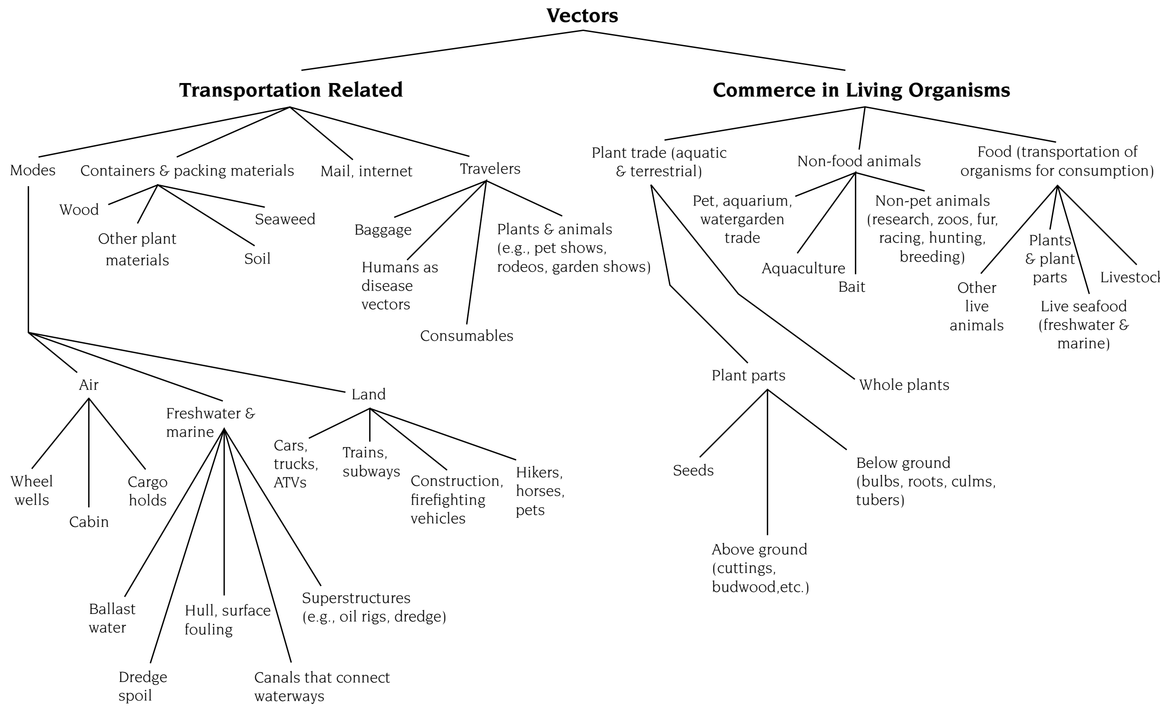

FIGURE 1.2.
Vectors by which nonindigenous species enter the United States and are transported within the United States. Reprinted from Lodge et al. (2006), with permission of the Ecological Society of America.

widely and become abundant at many new locations. Such species—roughly 0.3% of introduced plants and up to 25% of introduced animals (as calculated from the numbers above)—cause undesirable environmental and/or economic changes and are categorized as invasive. By definition, invasive species, which are a subset of nonindigenous species, are bad.

Policy and management implications become clear when these underlying processes and probabilistic transitions during invasion are recognized. The possible human management responses narrow as any invasion progresses (figure 1.1). As illustrated by the above vignettes, prevention is possible only early in the process, before a species arrives in a new range or at the point of entry. Eradication depends on the rapid convergence of appropriate technology, political will, and resources. Once a species is well established, eradication is costly and sometimes impossible. When the opportunity for eradication has passed, only two options remain: control of populations in selected locations, and adaptation by humans.

In most countries, including those in North America, adaptation has been vastly more typical than any other response, except when pests or pathogens have threatened either humans directly or highly valuable agricultural crops. Apart from these exceptions, we passively suffer the consequences of invasions. In the last decade, however, investments in eradication, control, and finally prevention have increased for natural ecosystems, and policy discussions in the United States and elsewhere increasingly feature prevention efforts.

In this book, we assess current scientific capability to forecast the identity, spread, and impact of potential invasive species. In chapters 3–6 we address the series of transitions represented in the left column of figure 1.1. Furthermore, we explore how ecological forecasting can be used in risk assessment and risk management of invasive species, testing especially whether cost-effective approaches, including prevention, can be identified.

Interest in prevention necessarily focuses attention on vectors (figure 1.2). Vectors are commercial activities driven by human desires for the benefits from increased trade. In the absence of strong efforts to prevent invasions, increasing trade will increase invasions. The numbers of nonindigenous plant pathogens, insects, and mollusks discovered in the United States since 1920 are strongly correlated with importation of goods over the same time period (figure 1.3). Trade with many countries is increasing (figure 1.4), and documented invasions are increasing in marine, terrestrial, and aquatic ecosystems (Ricciardi 2006; figure 1.5). Different vectors operate at different spatial scales and with different potential management interventions. Detailed knowledge of vectors, as well as of different taxonomic groups of organisms, must be combined in biological and economic models if they are to guide management and policy to cost-effectively reduce damages from invasive species.

Feedbacks: Economic Activity, Biological Processes, and Damages from Invasion

A circle of feedbacks exists between ecological processes and economic processes (figure 1.6): the economic benefits of trade drive invasions, invasions cause negative

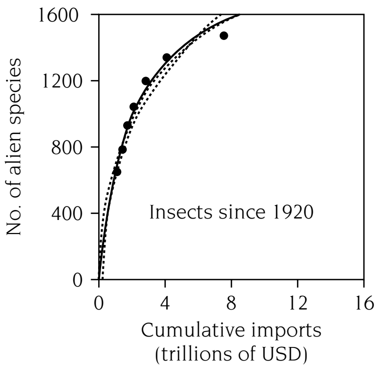

FIGURE 1.3.
Total imports into the United States since 1920 (measured in dollars) as a potential driver of cumulative invasions by terrestrial insects in the United States since 1920. Modified from Levine and D'Antonio (2003).

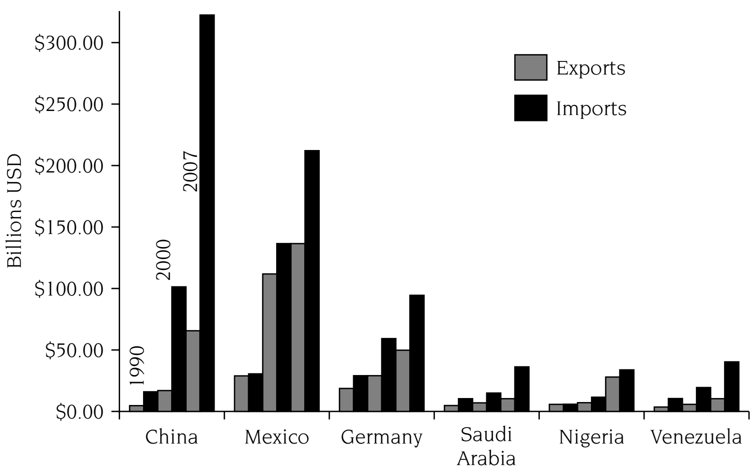

FIGURE 1.4.
Changes in total trade volume between selected countries and the United States, 1900–2007. First bars for each country are imports/exports during 1990; subsequent pairs of bars are for 2000 and 2007, respectively. Data from the U.S. Department of Commerce (2008).

economic and environmental impacts, and human perception of those impacts feeds back as management or policy initiatives to reduce trade or at least reduce the negative side effects of trade. Another way to look at this situation is as an adaptive loop, among risk assessment, risk perception, and risk management, that changes the risks to be assessed. A distinctive strength of this book lies in applying a combination of ecology and economics, with strong mathematical and statistical foundations, to management and policy questions.

Economics and the biological sciences have many similarities. Both are disciplines of limits—both examine how species deal with scarcity. Whether it is a human's reaction to a limited budget and unlimited wants or a squirrel's response to limited food and unlimited appetite for reproduction, all species deal with limits.

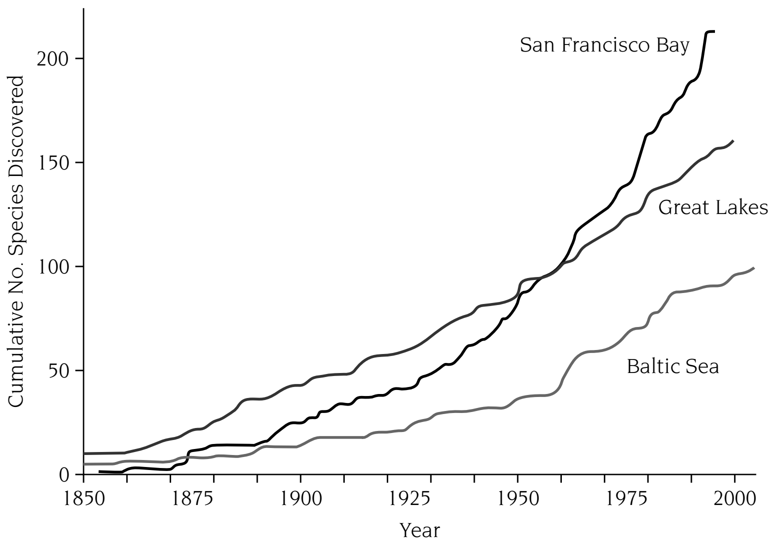

FIGURE 1.5.
Cumulative number of nonindigenous species that have been discovered in three major aquatic ecosystems in the last 150+ years. It is not known how many species remain undiscovered in each ecosystem, or how long the discovered species had been present before they were discovered (Costello et al. 2007). Nevertheless, the data suggest strongly that trade and/or other mechanisms by which humans cause the movement of species (e.g., canal construction) have caused an increasing number of invasions. Data from Cohen and Carlton (1998), Ricciardi (2001), and http://http://www.corpi.ku.lt/nemo/).

These limiting factors, as defined within both economics and the biological sciences, drive research efforts. Yet failure to account for joint influences on these limits in economic systems and biological systems can cause inaccurate perceptions of how each system works and provide misleading policy guidance. The idea of joint determination applies: links between the biological and economic systems create a progression of natural and human actions and reactions, in which a feedback loop emerges. Disturbances in one system set off repercussions in the other system, and these repercussions feed back into the system where the disturbances originated (e.g., Daly 1968; Clark 1990; Crocker and Tschirhart 1992; Sohngen and Mendelsohn 1998; Wilson 1998; Shogren and Crocker 1999; Dasgupta et al. 2000; Finnoff and Tschirhart 2003).

The impact of invasive species is a good example of joint determination. Thresholds for expansion of invasive species are functions of the present distributions and trends of their populations, their interactions with habitats, and the economic circumstances that cause introductions of additional individuals and the quality of potential habitat (e.g., fragmentation). Important economic circumstances include the relative prices of alternative sites for economic development and relative wealth of the landholders in the area. Sites with low relative returns in their “highest and best” use are

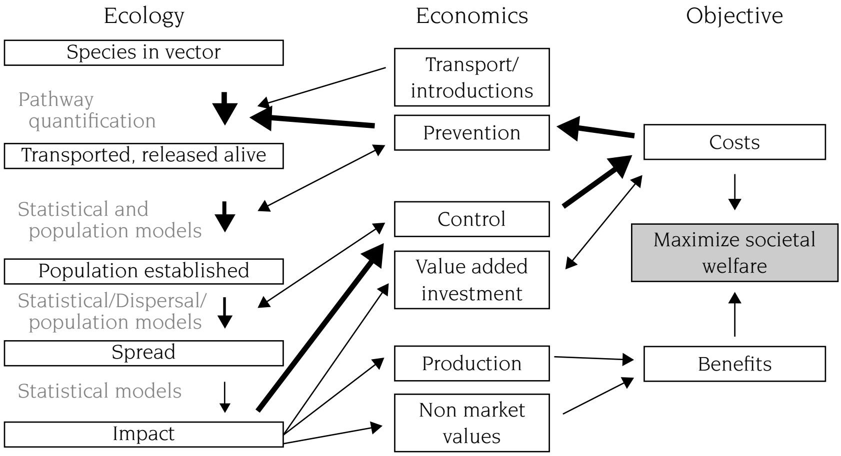

FIGURE 1.6.
Feedback between ecological processes (left column) and economic processes. The lightface text indicates the variety of tools, many recently developed or applied, that we use to model and forecast different stages of invasion. The bold arrows indicate possible feedback pathways in which damages from an invasion cause humans to change investments to reduce future damages: the impact of a species is expressed in increased control costs; in response, humans increase prevention expenditures that reduce the number of organisms entrained in the responsible vector. Modified from Leung et al. (2002).

more likely to be left undisturbed. Moreover, the rich can better afford to set aside undisturbed habitat that may be less susceptible to invasions.

These interactions demonstrate that invasive species establishment and spread are determined by both economic and biological parameters. Effective models of the spread and impact of invasive species require natural and social scientists to integrate their respective tools and their indicators of success and failure. Integration across disciplinary boundaries is especially crucial when a proposed policy may trigger a political feud fueled by misperceptions of benefits and costs imposed on natural and social systems. The resulting challenge is to integrate models, methods, and mind-sets to help researchers and decision makers better understand and manage the delicate balance between private rights of self-determination and social rights to environmental protection.

The most straightforward and pragmatic method is to form a research team that includes both economists and ecologists to construct an explicit model to estimate the trade-offs associated with alternative policy options. Models are always abstractions and must never be mistaken for reality. Nevertheless, the integrative thought process of model construction focuses attention on the most important links between systems. The differences and similarities between economics and ecology can be addressed directly by forcing researchers to construct and link the human and natural sectors of the model. A linked model can then provide informed guidance for pragmatic choices among the trade-offs necessarily involved in policy making.

We illustrate this approach using a model that captures the risks posed by one invasive species, lake trout (*Salvelinus namaycush*), on one endangered species, the cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake in Yellowstone National Park, Wyoming. Settle et al. (2002) explored how feedbacks between humans and nature affect the likelihood of the desired result—an increased population of cutthroat trout, because many more anglers prefer to catch cutthroat. In a dynamic modeling framework, Settle et al. incorporated both economic and ecological flows and reciprocal flows between the two systems. To test the importance of the economic-ecological feedbacks, the authors compared the modeling results with and without the reciprocal flows between the two systems. They considered two scenarios: (1) a *remove-all-lake-trout* scenario, in which lake trout are immediately removed from Yellowstone Lake; and (2) a *leave-the-lake-trout-be* scenario, in which lake trout are left alone to reach a steady state within the Yellowstone Lake ecosystem.

Under the remove-all-lake-trout scenario, the steady-state population of cutthroat trout is about 2.7 million and 3.4 million, without and with feedbacks. Without feedback between the economic and ecological systems, park visitors continue to fish as before, putting constant pressure on the cutthroat. With feedback, visitors react to declining cutthroat populations by fishing less and visiting other attractions more. This behavioral reaction by park visitors, which reflects an increase in what economists call the shadow price of fishing, now affects the ecosystem because a decline in fishing time produces an increase in the population of cutthroat. Incorporating feedbacks between the economic and ecological system produced estimates of a 26% larger population of cutthroat, the desired species.

Under the leave-the-lake-trout-be scenario, Settle et al. (2002) found a different result. Now a no-feedback model (fishing continued as before) suggested a more desirable outcome than would be likely to occur—almost 1 million cutthroat trout remain versus zero cutthroat trout when feedbacks were included. Without feedbacks, visitors continued to fish and acted as a control on the population of lake trout, even though it is an incidental catch. With feedbacks, visitors shifted away from fishing as the cutthroat trout population declined and the lake trout population increased, leaving the lake trout to take over as cutthroat were extirpated. Without incorporating feedbacks, policy advice might have led park officials to adopt the cheaper leave-the-lake-trout-be policy, satisfied that at least the cutthroat would continue to exist in Yellowstone Lake. According to the model by Settle et al. (2002), such a policy would likely have resulted in the disappearance of cutthroat. The National Park Service currently uses a policy of gill netting lake trout. (See chapter 2 for additional discussion of this example.)

This example illustrates how integrating the feedbacks between economics and ecology can be essential to provide appropriate advice for management and policy for invasive species. Technical integrated models can be a powerful tool to make the linkages among disciplines transparent and workable. Failure to account for the specific links between ecosystems and economic systems might lead to inappropriate management of either the ecosystem or the economic system. Integration of economics and ecology is fundamental both for science and policy. For science, integration