# Risk Analysis and Bioeconomics of Invasive Species to Inform Policy and Management

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Annu. Rev. Environ. Resour. 2016. 41:453–88

The *Annual Review of Environment and Resources* is online at environ.annualreviews.org

This article's doi:
10.1146/annurev-environ-110615-085532

## Keywords

forecasting, prevention, early detection, control, eradication, dispersal, surveillance, species distribution modeling, damage

## Abstract

Risk analysis of species invasions links biology and economics, is increasingly mandated by international and national policies, and enables improved management of invasive species. Biological invasions proceed through a series of transition probabilities (i.e., introduction, establishment, spread, and impact), and each of these presents opportunities for management. Recent research advances have improved estimates of probability and associated uncertainty. Improvements have come from species-specific trait-based risk assessments (of estimates of introduction, establishment, spread, and impact probabilities, especially from pathways of commerce in living organisms), spatially explicit dispersal models (introduction and spread, especially from transportation pathways), and species distribution models (establishment, spread, and impact). Results of these forecasting models combined with improved and cheaper surveillance technologies and practices [e.g., environmental DNA (eDNA), drones, citizen science] enable more efficient management by focusing surveillance, prevention, eradication, and control efforts on the highest-risk species and locations. Bioeconomic models account for the interacting dynamics within and between ecological and economic systems, and allow decision makers to better understand the financial consequences of alternative management strategies. In general, recent research advances demonstrate that prevention is the policy with the greatest long-term net benefit.

## Contents

## 1. INTRODUCTION

Ecologist Charles Elton (1) was motivated to write the seminal book on invasive species partly by the depredations of wartime Great Britain's food supply by nonindigenous rats and other pests. That applied motivation intersected in Elton's mind with ecological insights that spawned the field of invasion biology, which has fostered many research volumes (2), journals (e.g., *Biological Invasions*), and textbooks (3) that explore the patterns and processes by which nonindigenous species interact with indigenous species and ecosystems.

This body of basic ecological research has often had a confusing relationship with the applied dimensions of nonindigenous species. The history of humankind is replete with harmful impacts and beneficial uses of nonindigenous species (4, 5), making it possible for some scholars to emphasize that many nonindigenous species cause little harm (6), whereas others emphasize the large harms caused by many other species (7). These academic exchanges have spilled over into the popular press (8), confusing the public and policy makers about which invasion biology research is relevant to the policy and management of nonindigenous species (9, 10).

In the policy context, most of the apparently conflicting claims are obviated by accepting the US government's definition of invasive species, which emphasizes harm: "an invasive species is an alien [nonindigenous] species whose introduction does or is likely to cause economic or environmental harm or harm to human health" (11, section 1.f.). The definition in the Convention on Biological Diversity (CBD) (12) is similar but limited to nonindigenous species that threaten "biological diversity." In this review, we use the US government definition and understand that the harms referred to must be understood as net harms (some species bring a mixture of benefits and harms). Furthermore, given research advances since 1999, we conceptualize many of the objects of harm as natural capital, ecosystem goods, or ecosystem services, using ecosystem services as shorthand (13).

Applied research agendas from many disciplines aim to inform efforts to reduce the current and future harmful impacts of nonindigenous species on human health (14), forest and wildlife health (15), and indigenous biodiversity (16), as well as on the productivity of plant and animal species grown in agriculture (17), aquaculture (18), and forestry (19). Here, we bring these multiple basic and applied strands of research together, emphasizing the recent research advances in biology, economics, and technology that may be most helpful in improving the management and policy of nonindigenous species. We consider scales from global to local and emphasize long time horizons (decades to centuries) because they are most relevant to how human welfare is affected by biological invasions and the management of them (20).

Efficient management of invasive species requires risk analysis, which allows decision makers to choose management based on the probability and magnitude of damage under alternative management options, as well as on the cost of each option. For risk analysis, the invasion process can be conceptualized as a sequence of steps from initial introduction to establishment to economic impact (**Figure 1**, *left column*) (21, 22), with each step having an independent transition probability. For example, the probability of introduction ($P_{introduction}$) approaches 1 if a species is allowed in the pet trade (because releases and escapes of pets are so common) but may be much lower if the species is an occasional hitchhiker on the hull of a ship. In general: $P_{introduction} \times P_{establishment} \times P_{spread} \times P_{impact} = P_{harm}$. The probability of harm multiplied by the predicted magnitude of harm provides the expected value of damage against which a decision maker would compare the cost of a management action to reduce one or more probabilities in the sequence of transition probabilities leading to $P_{harm}$. Choosing the best mix of management interventions requires an accounting of these transitions so that the expected marginal gains of each management option can be weighed against the expected marginal costs.

Under the best of circumstances in practice, the manager's tool box allows choices about how much to invest in each of three management categories: (*a*) actions to reduce the probability of introduction, (*b*) information gathering (e.g., surveillance) to discover newly introduced or established populations, and (*c*) actions to eradicate or reduce established population(s) (i.e., control) (23). Under more typical circumstances, the manager often has authority to deal with only one or two of the transition probabilities. For example, given an ongoing invasion that came originally from a neighboring jurisdiction ($P_{establishment} = 1$), the manager can decide only how much to invest in information gathering (e.g., analyses to determine where the species might spread next, and surveillance) and how much to invest in control.

Conceptualizing the invasion process in this way highlights that preventing invasions requires management of pathways at the beginning of the invasion process and that reducing harm during later invasion stages is more difficult and expensive (**Figure 1**). Although considering the entire

| INVASION PROCESS | RESEARCH ADVANCES | informing POLICY GOALS | and MANAGEMENT EXAMPLES |
|---|---|---|---|
| **Introduction** | Assess risks of pathways<br>• Commerce in living organisms (e.g., pets, horticulture)<br>• Transportation vectors carrying many unknown species (e.g., planes, trucks, ships and boats)<br>Quantify effectiveness/costs of alternative management | **Prevent arrival, release, or escape** | Pre-import approval for specific species; lists of allowed, prohibited, watch species<br>Fumigating wood packing material; shipboard ballast water treatment<br>Prioritize prevention by benefit:cost |
| **Establishment** | Develop new technology to detect rare species (e.g., eDNA, remote sensing)<br>Design cost-effective sampling regimes over space and time<br>Discover/develop taxon-specific eradication technology | **Early detection, eradication** | Expanded surveillance programs with new technology<br>Deploying new eradication technologies for wider range of taxa |
| **Spread** | Discover what limits species distributions<br>Identify potential habitat with improved species distribution modeling (SDM)<br>Quantify effectiveness and costs of alternative management | **Slow the spread** | Prioritize inspection, interdiction based on:<br>• Pathway linkage of infested areas to suitable uninfested areas<br>• Cost effectiveness of preventing egress from infested area (e.g., quarantine) versus preventing ingress to high-value areas<br>• Value of avoided losses versus cost of management |
| **Ecological/health impact**<br>**Economic impact** | Discover/test new control technologies (e.g., gene drive)<br>Implement ecosystem services and bioeconomic modeling in forecasts of impact and alternative management scenarios<br>Quantify effectiveness/costs of alternative outreach, education, and engagement with the public | **Control, adapt** | Field test and deploy more control technologies<br>• Chemical<br>• Genetic<br>• Mechanical |

Arrow width reflects the declining number of species reaching each stage of invasion

**Figure 1**

Conceptualizing invasions as a process (*left column*) that includes multiple steps involving human behavior and the biology of other species helps to identify research priorities (*second column*), policy goals (*third column*), and management interventions (*right column*) that are most relevant to each step in the invasion process. Abbreviations: eDNA, environmental DNA; mgmt, management; tech, technology.

sequence of transitions is appropriate for a pathway or for a species that has not yet been introduced, this conceptualization also emphasizes that a risk assessment (RA) can begin at any stage of invasion and may consider all subsequent probabilities to help identify which management interventions are most appropriate at a given stage of invasion.

Because each of the transitions in the invasion process is often associated with otherwise beneficial commerce or transportation, we emphasize throughout the review case studies of ecological forecasting and risk assessment that quantify dynamic interactions between the ecological and economic systems. A risk analysis approach provides a framework for considering the benefits and harms of both the pathway and any management actions under consideration (24, 25). Hence in most wealthy countries, pharmaceuticals for humans and livestock are subject to intensive risk assessments, including clinical trials, before risk management decisions are made about market access for new drugs (26). The production, harvesting, and processing of food intended for humans are governed by risk analysis of toxins, pathogens, and parasites (27). For humans, livestock, and crops, the risk of spread of infectious disease is effectively managed by vaccines and other risk-reduction behaviors, including quarantine. In the 2003 global severe acute respiratory syndrome (SARS) epidemic, scientific research identified the causal virus, assessed the risk factors in its global dispersal, designed and implemented risk management practices within the context of existing national and international public health authorities, and eradicated the invasion—all within eight months (28). Risk analysis was also the foundation of the successful control of the 2014–2015 Ebola outbreak (29). Since research and technological developments enabled an understanding of these risks and how they could be reduced, most societies no longer accept unmanaged risks of pharmaceuticals, food production, and infectious disease.

When it comes to invasive species, however, most societies still tolerate mostly unmanaged risks despite mounting damages (30), in part, because only in the last three decades has the invasive species research community adopted the risk analysis framework and produced practical risk management technology and decision support tools (31). Management efforts that are wholly or partly successful are increasing. Examples include preventing importation of invasive plants into Australia (32) and brown tree snakes into Hawaii (33), reducing aquatic invasions from ballast water (34), reducing terrestrial insect invasions from wood packaging material (35), improved detection of incipient invasions (36), eradication of invasive mammals on islands (37), and eradication of invasive *Caulerpa* seaweed and *Spartina* cordgrass in coastal habitats (38), as well as slowing the spread and improved control of gypsy moths and other insects (19). Overall, however, policy and management are lagging behind research and development. Our goal is to review recent advances at the science-management-policy interface to help policy and management catch up.

In Section 2 below, we review the policy frameworks at international and national scales that enable or constrain management of invasive species. We organize the remainder of the review around the major steps through which an invasive species passes from initial introduction through establishment to economic impact (**Figure 1**). In Sections 3–8, we synthesize and offer examples of recent research that quantifies risks of harm and how research results have or could inform improvements in management. In Section 9, we emphasize the importance of quantifying and communicating uncertainty. Throughout, we emphasize how recent research has or could improve policy and management strategies.

## 2. INVASIVE SPECIES POLICIES

Damages caused by invasive species have motivated an international policy framework on the basis of trade, environmental, and transportation agreements. This compartmentalization of policies developed because pathways of species introduction involve different commodities, consumer goods, and packaging, as well as diverse modes of transportation. In addition, species affect a diversity of economic, environmental, and public health interests. Coordinating agreements across pathways and impacts has increased over recent years as member countries streamline resource use and avoid conflicting policies. Existing agreements largely focus on the movement of invasive species between countries and the legal measures that can be taken to manage pathways of introduction. Management activities addressing invasive species within a country—after introduction to the country has occurred (**Figure 1**)—are left to national authorities.

### 2.1. Trade Policies

At the international level, concerns about invasive species arose primarily from the tension between protecting domestic agriculture and livestock from pests and diseases and the desire to ensure export markets for such products. In 1994, under the World Trade Organization (WTO), a series of agreements, including the Agreement on the Application of Sanitary and Phytosanitary Measures (SPS Agreement), set binding requirements (e.g., use of science, risk assessment, minimal impacts on trade, transparency) for establishing national regulations to protect human, animal, and plant life and health from risks associated with invasive species, pests, and pathogens. The SPS Agreement embodies the strongest existing international policy guidance on invasive species, although the words invasive species do not occur in the agreement. It encourages countries to harmonize their national requirements through international standards developed by the International Plant Protection Organization, the World Animal Health Organization, and the Codex Alimentarius Commission.

Although the WTO agreements establish the basic framework of international trade law, efforts to update them have stalled (39, 40), resulting in a shift toward trade agreements that are regional rather than global. For example, the United States has negotiated many bilateral trade agreements and others including the North American Free Trade Agreement, the Central American Free Trade Agreement, and most recently the Trans-Pacific Partnership (TPP). Several of these agreements address invasive species in associated environmental programs and reviews, while the TPP addresses invasive species in the agreement itself. Ongoing negotiations between the United States and the European Union on the Transatlantic Trade and Investment Partnership may also directly address invasive species because the European Union has included invasive species in their list of priority sustainable development issues (41).

### 2.2. Transportation Policies

The International Maritime Organization (IMO) has addressed the international transport of invasive species in and on ships. The International Convention for the Control and Management of Ships' Ballast Water and Sediments is a binding international agreement, which as of May 2016 had not come into force (42). The IMO has also developed voluntary guidance on the management of biofouling to reduce the transport of organisms on the outside of ships (43). No binding international agreements are in place to address invasive species in other transportation vectors (e.g., airplanes, trains, and trucks that cross international borders).

### 2.3. Environmental Policies

International environmental law addressing invasive species is less developed and mostly voluntary. The 1992 CBD is the key international environmental instrument addressing invasive species, which are included as a strategic goal within the Aichi targets (44). CBD's guidance on invasive species is often reflected in other environmental agreements, including the Convention on Migratory Species and the Ramsar Convention on Wetlands of International Importance.

Although trade agreements provide a basis for regulating sanitary and phytosanitary (SPS) issues associated with invasive species, they do not identify the specific risks that countries should address. CBD and other environmental agreements partially fill this gap with voluntary guiding principles for invasive species, including the risks associated with pets, aquarium and terrarium species, live bait, and live food (45, 46). Efforts to improve international legal coordination on invasive species are occurring in the Inter-Agency Liaison Group on Invasive Alien Species, which brings together staff from relevant institutions, including CBD, WTO, and IMO (47).

### 2.4. Policy Integration at the National Level

Increased coordination is useful across international agreements, but policy implementation falls to national governments. New Zealand, Australia, and the United States maintain relatively strong domestic systems, and recent legislation in South Africa, Norway, and the European Union better addresses the harms from invasive species. In the 1990s and early 2000s, many believed that

## US FISH AND WILDLIFE SERVICE RAPID RISK ASSESSMENT

The USFWS has developed a protocol for risk assessment that allows nonindigenous species to be assessed in a matter of hours. RAs are based on the history of invasion elsewhere, whether the species carries one or more diseases, and a climate match between the current range of the species and the United States (210; B.G. Marcot, M.H. Hoff, C.D. Martin, S.D. Jewell, C.E. Givens, unpublished information). A climate match is assessed using the new Risk Assessment Mapping Program (S. Sanders, C. Castiglione, M.H. Hoff, unpublished information), which predicts suitable climates for the species at different points in the future (current year, 2050, and 2070). This risk assessment tool has passed review by the US Office of Management and Budget (211) and supports the service's efforts to identify and respond to invasive species threats and climate change. Results are being made available for use by states, live animal importers, researchers, and other interested parties.

trade rules had a chilling effect on national environmental regulations (48). The SPS Agreement was depicted, for example, as reactive and ill-equipped to deal with issues of uncertainty and the precautionary approach (49, 50). More recently, improvements in risk assessment techniques, such as those described in the sections below, have strengthened the scientific basis for decision making concerning import regulations for non-native species and have allowed more stringent regulations that are consistent with SPS requirements.

In New Zealand, importation of any product (including its vector, e.g., shipping containers) that could contain a pest is contingent on a risk analysis, which can result in the establishment of an Import Health Standard detailing necessary conditions for import. In the United States, the responsibility for conducting risk assessments is divided across federal departments. The US Department of Agriculture's Animal and Plant Health Inspection Service is responsible for assessing threats to plant health, including the determination of plants, plant pests, and diseases that are barred from import. The Animal and Plant Health Inspection Service recently implemented provisions under its Q37 regulations[1] to screen or identify potentially risky plant species that are barred from import pending a full risk assessment. The US Fish and Wildlife Service (USFWS) is responsible for identifying injurious wildlife (species posing a threat to wild mammals, birds, fish, mollusks, crustaceans, amphibians, and reptiles) that should be barred from import into the United States. USFWS increasingly uses formal, recently developed risk assessment procedures to identify species to bar importation (see the sidebar US Fish and Wildlife Service Rapid Risk Assessment). Finally, an EU Directive of 2014 provided a comprehensive approach to prevention and management, including a list of invasive alien species of EU concern (51). Species are added to the list by the European Commission on the basis of a risk assessment, including petitions and supporting assessments submitted by Member States. These examples show how some countries are using SPS provisions, including science-based risk assessments to advance environmental protection and economic interests.

Ecuador, Mexico, and other developing countries in Africa, the Caribbean, the Pacific, and Southeast Asia are also developing management and regulatory programs, often aided by investments from the Global Environment Facility, e.g., its GloBallast project on ballast water. With international legal underpinnings in place, countries can use the information, tools, and policy experience of developed countries and risk assessment approaches described in subsequent sections of this review to reduce the harm from individual species and pathways.

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[1] See the United States Department of Agriculture web page: **https://www.aphis.usda.gov/aphis/ourfocus/planthealth/import-information/permits/plants-and-plant-products-permits/plants-for-planting/ct_q37restructure/**.

### 2.5. Emerging Research Questions Regarding International Agreements and National Practices

With WTO negotiations at a standstill, the most significant international guidance on invasive species is likely to derive from environmental agreements, and possibly bilateral and regional trade arrangements.

1. What kinds of invasive species risk assessments are likely to be most acceptable as components of regional trade agreements, and how might that depend on the member countries in a given agreement?
2. What types of risk assessments and decision support tools can best leverage developing countries' efforts to prevent invasive species introductions within their trade and SPS regulations?

## 3. ACCURATE SPECIES RISK ASSESSMENTS FOR MANAGEMENT

The two major categories of vectors of species introduction are commerce in living organisms (e.g., the horticulture, aquaculture, pet, and live food trades) and transportation (e.g., shipping-related ballast discharges and biofouling, canals, airplanes, and terrestrial vehicles). A fundamental difference between these categories is that the species involved in commerce are or could be known. It would be desirable to exclude from commerce all invasive species while allowing noninvaders because they provide benefits. In contrast, transportation vectors unintentionally entrain species, and it is rarely known which species are being transported. Because there is no anticipated benefit from unintentionally introduced species, management can focus on excluding all such species without even knowing their identity.

In this section, we describe a class of decision-making tools, i.e., trait-based risk assessment tools, which can be used to predict the invasiveness of known species before they are introduced. These tools are most useful for commerce in living organism vectors. However, they can also be applied to transportation vectors, e.g., to prioritize ships coming from regions where high-risk species are known to occur, for greater management. We review the development and growing number of trait-based RAs that are increasingly accurate for many taxonomic groups. Bioeconomic analyses demonstrate that such tools, if used in a risk management program over a long enough time horizon, can drive overall increases in ecosystem services and human well-being because invasions of potentially harmful nonindigenous species are prevented while commerce in most benign species continues (32).

### 3.1. Development and Accuracy of Trait-Based Risk Assessments

In possibly the first effort to classify species as invasive on the basis of their traits, Baker (52, 53) published a list of 12 characteristics of the ideal weed. On this foundation, modern risk assessment tools identify traits and trait complexes that are consistently associated with invasiveness. When robust patterns are found, they can be used to predict invasion risk for species that may be introduced in the future. An ideal risk assessment tool would be rapid so that the many species in trade can be assessed, have high accuracy so that the results offer a reliable guide to the true impacts of a species, and be consistent so that multiple users assessing the same species reach the same outcome.

A range of approaches to trait-based risk assessment has emerged in recent decades. The most intensive of these requires detailed and extensive information about a species to predict its distribution and impacts should it become established (54). This approach is rarely used because it takes months to years to assess a single species. In addition, its accuracy and consistency are difficult to assess.

More rapid approaches have been developed in recent decades, including those based on responses to expert-informed questionnaires. These questionnaires, which usually comprise ~15–50 questions, are developed using the intuition of experts about which traits make a species invasive. Answers are scored, and the prediction for a species is determined by whether the sum of these scores exceeds a predetermined threshold based on the risk tolerance of the decision maker. Many regional and national risk assessment tools use this approach (55).

More recently, statistical and machine learning approaches, including logistic regression and classification and regression trees, have been used to construct trait-based RAs (31, 56, 57). Algorithms identify patterns in trait data that are consistently associated with invasiveness. As with the questionnaire approach, these patterns can be applied to species that may be introduced in the future. Statistical RAs typically require data about only one to seven traits.

Supplemental Material

Questionnaire and statistical tools have high accuracy (75–92%) across a range of taxonomic groups, habitats, and regions (58); see **Supplemental Table 1**. Follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**. Accuracy can be estimated by assessing species that have previously been introduced and for which the invasion outcomes are known. For statistical tools, this is usually done with leave-one-out cross validation. These questionnaires and statistical risk assessment tools can often be applied with high accuracy to multiple regions. For example, the Australian Weed Risk Assessment (59) is a questionnaire approach that is accurate in regions beyond Australia (55), and modifications of the New Zealand Aquatic Weed Risk Assessment are accurate for the United States and the binational Laurentian Great Lakes region (60).

The final risk assessment approach reviewed here is based on only two components: (*a*) how similar the climate in a species' native environment is to the climate in the recipient environment and (*b*) the species' history of invasion elsewhere. To test the accuracy of this approach, R.P. Keller (unpublished information) gathered data on the 154 non-native freshwater fish species that have been introduced to the continental United States. The impact of each species was known and categorized as (*a*) failed (no established populations), (*b*) established with no impacts, (*c*) established with minor impacts, or (*d*) established with major impacts. History of prior establishment elsewhere and climate match were gathered for each species and used in a rapid risk assessment framework to determine the percentage of species in each impact category that would have been predicted invasive at the time they were first recorded in the United States. Sixteen percent of species in category *a* would have been predicted invasive, along with 22%, 62%, and 74%, respectively, of species in the other categories. Thus, most noninvaders would have been predicted to be benign, and most invaders would have also have been correctly predicted. This relatively high performance using only two kinds of data suggests a role for this cheap approach either as a stand-alone tool or as an initial part of a hierarchical risk assessment system. The sidebar US Fish and Wildlife Service Rapid Risk Assessment describes the development and use of a similar tool by the USFWS.

## 3.2. Data and Risk Assessment Tool Availability

Several large databases of species traits, ranging from global (e.g., TRY, a global database for plant traits) (61) to national (e.g., Fish Traits, a database for freshwater fish in the United States) (62), have recently become available. Since these data have become available for the taxa and region of interest, the time for risk assessment development has been drastically shortened. For example, a statistical risk assessment for freshwater fish in the Laurentian Great Lakes (63) was developed in one year using data available in Fish Traits and FishBase (64) and high-resolution climate data available in CLIMATCH (65). This risk assessment was then used to screen >750 species that are not yet in trade in the region (63). Easy and cheap access to advanced statistical and machine learning methods has also increased through open-source software like R, and methods like Classification and Regression Trees and Conditional Inference Trees, which can incorporate many types of imperfect data and rapidly produce user-friendly decision trees that are easy for nonspecialists to apply.

## 3.3. Economic Outcomes from Risk Assessment

The economic outcomes from applying risk assessment depend on rates of false-positive predictions (i.e., benign species predicted to be invasive), false-negative predictions (i.e., invader predicted to be benign), and the costs of each type of error. False-positive predictions are usually more common because, for most taxonomic groups, the number of noninvasive species is much greater than invasive species. This base rate effect underlies concerns that using risk assessment will produce a greater loss of benefits (from wrongly excluding noninvasive species from commerce) than any gain in benefits (from correctly excluding the smaller proportion of invasive species) (66). However, recent analyses that explicitly consider both types of errors and their costs demonstrate that RAs produce net economic benefits (32, 67, 68). Two major conditions, which are likely to be generally true, drive this result.

First, allowing additional species into trade increases the total value of trade minimally because consumer spending in these markets is not limited by choice (67). Second, damages per invasive species are extremely high relative to the benefits per species in trade. Risk assessment tools at current levels of accuracy are thus sufficient to produce economic benefits—in addition to the obvious environmental benefits—for an importing region or nation.

Despite its benefits, risk assessment is currently used only by a few wealthy nations, and in those nations, risk assessment programs are defensive measures designed to protect the importing nation. An international system discouraging exporters from sending species to regions where they may become invasive would bring global benefits and would provide protection to poorer countries that currently have no risk assessment system to protect themselves (69).

## 3.4. Emerging Research Questions Regarding Trait-Based Invasive Species Risk Assessment

1. What are the relative cost, accuracy, and consistency of questionnaire and statistical or other alternative risk assessment approaches?
2. What are the barriers in national and international governance that limit development and adoption of risk assessment by both importers and exporters to prevent invasive species from entering global trade?

# 4. FORECASTING VECTORS, INTRODUCTION SITES, AND DISPERSAL

Whether a species escapes after intentional importation or after incidental transport, management priorities depend on forecasting where the species will spread next. The initial introduction of invasive species results from anthropogenic pathways operating on global to local scales, whereas secondary spread often results from a combination of anthropogenic pathways and natural dispersal mechanisms (**Figure 2**). Early invasion biologists focused on predicting natural dispersal after a species was introduced (70), but much current research incorporates models of anthropogenic vectors to inform prevention and other management efforts (71).

The global airline and shipping pathways (**Figure 2**) transport billions of living organisms intentionally (including fish, birds, mammals, and living plants in the pet and horticulture industries) and many hitchhikers (including rats, biofouling organisms, insects, and diseases); models of these can inform policy and management. Models of the global airline network have been used to forecast the spread of emerging infectious diseases and have helped prioritize airports for travel restrictions to slow their spread, e.g., SARS (72) and Ebola (79). Likewise, models of the global shipping network identified hotspots of potential introductions for freshwater and marine species from ballast water (73, 80) and biofouling (81), which can help prioritize high-risk ports or shipping routes for monitoring or management (82). The GloBallast Partnership (**http://globallast.imo.org/**) uses such models to identify priority subregions for program implementation and in their management recommendations for ship inspections. Such targeting of higher-risk trade networks (e.g., 83) for more intensive management can more efficiently reduce invasion impacts than untargeted trade management or attempts to reduce postinvasion dispersal.

After introduction via a global transportation network, secondary spread often occurs at regional and local scales by additional anthropogenic vectors and natural dispersal (**Figure 2**). For example, lionfish were first discovered in Florida in the early 1990s (84). Biophysical models have since predicted the spread of lionfish throughout the western Atlantic Ocean via natural dispersal mechanisms and have guided management responses (85). One of the goals of the National Invasive Lionfish Prevention and Management Plan for the United States is to use analyses of pathways to identify high-priority sites for surveillance and management (**Figure 2**). For forest pests, such as the gypsy moth (**Figure 2**) (77), emerald ash borer (*Agrilus planipennis*) (86), and others (87), models of natural dispersal have been coupled with cost-benefit analyses to guide decisions among alternative management strategies. The ongoing Slow the Spread program for gypsy moths prioritizes locations for management on the basis of damages (e.g., timber, recreation, residential property values), spread models, and the costs of management (**Figure 2**) (88).

Global shipping introduced dozens of species into the Laurentian Great Lakes (89), from whence many have dispersed much more widely (90). Models have subsequently demonstrated—and in some cases predicted—how anthropogenic dispersal mechanisms, including local shipping and recreational boating (78, 91), and natural dispersal via stream networks (92) have caused spread of dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*; **Figure 2**), spiny water fleas (*Bythotrephes longimanus*), Eurasian watermilfoil (*Myriophyllum spicatum*), and other species from the Great Lakes across the United States (93). The explanatory power of these models and correct predictions, such as the prediction that Lake Mead was likely to become infested with dreissenid mussels shortly before they were found there (78), resulted in outreach campaigns, boat inspection programs, and other containment measures (94). These models have also been used to evaluate alternative management strategies to prevent the spread of invasive species on a regional scale (95, 96). In particular, they shifted the sole focus of management in many jurisdictions from protecting uninfested habitats to a more cost-effective balance, including preventing species from leaving infested habitats (97).

Within the Laurentian Great Lakes, models of shipping and natural dispersal by currents have been used to guide surveillance efforts and to assess potential management activities. The identification of monitoring locations for Eurasian ruffe (*Gymnocephalus cernuus*) was informed by a model of the Great Lakes shipping network (91), which resulted in positive eDNA detection in new areas (98). A model of the natural dispersal via currents in Lake Michigan was informed by the shipping model to identify potential sites of midlake ship ballast water exchange that would reduce

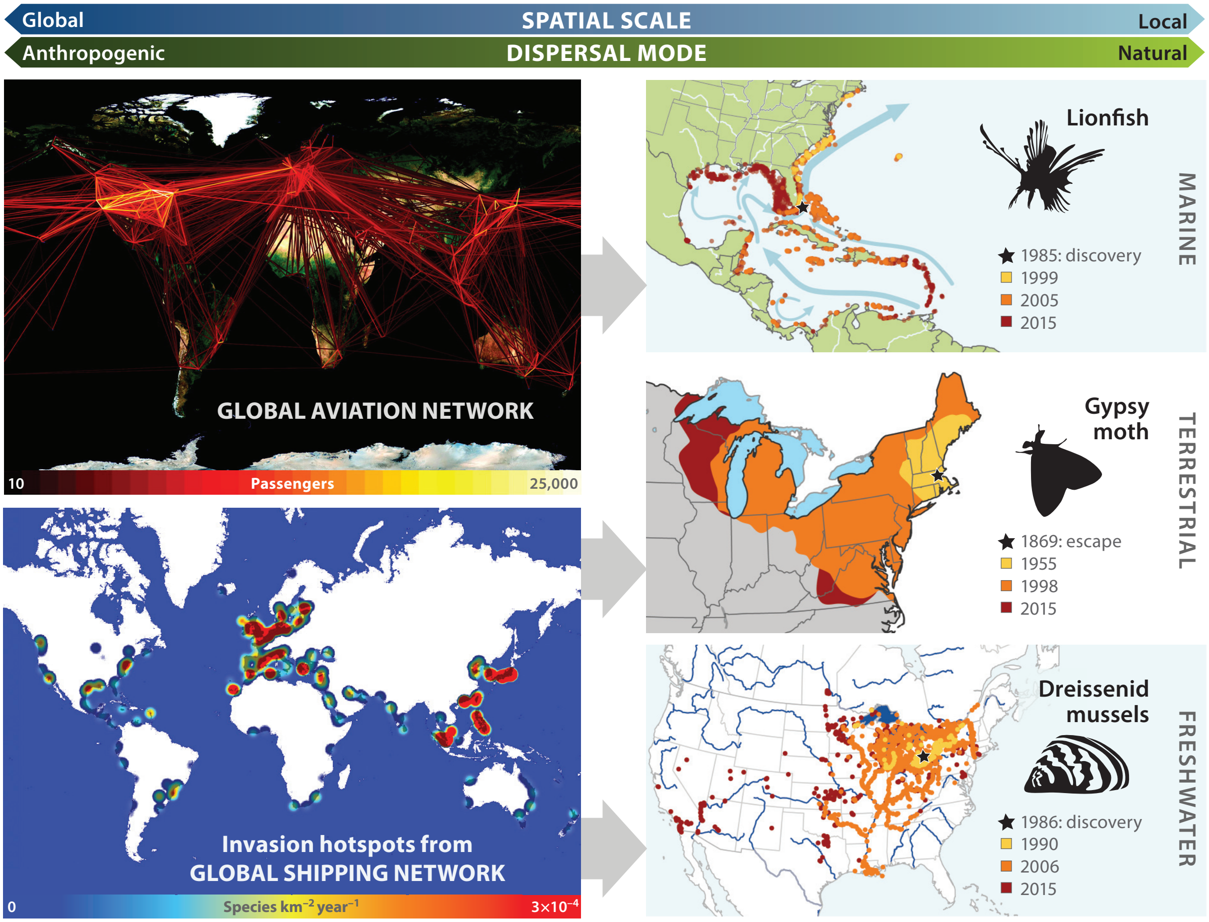

**Figure 2**

Effective management of invasion pathways requires conceptualizing them as a continuum of global to local dispersal (*top bar*), first necessarily by anthropogenic vectors (to overcome intercontinental barriers) and finally including natural dispersal mechanisms (*lower bar*). The anthropogenic vectors that drive intercontinental invasions are airline flights (major routes of the airline network are shown) (72) and the marine shipping network (predicted invasion hotspots resulting from marine routes) (73). Indo-Pacific lionfish were introduced into North America via airline delivery for the pet industry, with subsequent release or escape and initial establishment (*black star*) near Miami (74) and dispersal in the Atlantic Ocean, Caribbean Sea, and Gulf of Mexico by natural activities, including hurricane-driven currents (75, 76). The Eurasian gypsy moth escaped from Medford, Massachusetts, (*black star*) following intentional shipboard transport, with natural dispersal driving subsequent spread, which is substantially slowed by an ongoing government program involving surveillance and control (77). Eurasian dreissenid mussels (zebra mussel and quagga mussel) were first discovered in the Laurentian Great Lakes (*black star*), transported there in ships' ballast water, and subsequently spread within the Great Lakes via ships and natural dispersal via currents, escaped into the Mississippi River basin via the Chicago Sanitary and Ship Canal, and crossed terrestrial landscapes on recreational boats and trailers. From Lake Mead, Arizona, artificial waterways and boaters enabled dispersal to other parts of the US West (78). Lionfish and dreissenid mussel data are from US Geological Survey (P. Schofield, A. Benson); gypsy moth data are from Slow the Spread Foundation 2015. Global aviation map (72), copyright (2004) National Academy of Sciences, Washington, DC.

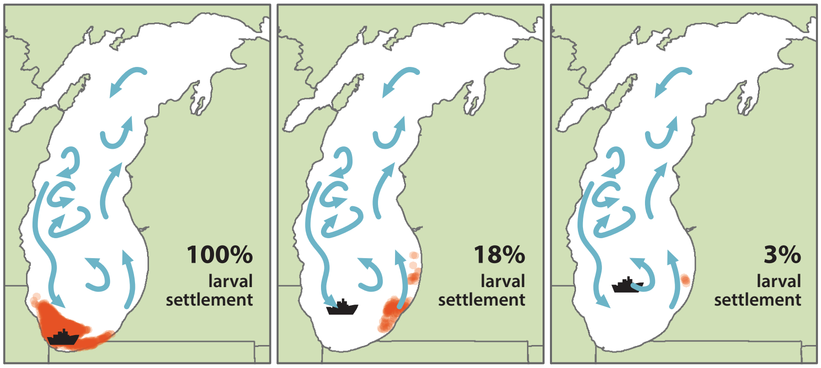

**Figure 3**

Simulated settling of planktonic larvae of golden mussel (*orange*) dispersed by currents to suitable nearshore habitats from ship deballasting locations (*black icons*) representing the Port of Chicago (*left*) and two offshore points. Blue arrows represent the observed mean summer currents (99). Results suggest that the probability of establishment of an invasive species from releases of planktonic larvae could be substantially decreased by deballasting at particular offshore locations. Reprinted and modified with permission from 100 and 101.

the risk of spread to shoreline habitats of any planktonic invasive species (e.g., larval Eurasian ruffe, golden mussel) discharged in ballast (**Figure 3**).

### 4.1. Multijurisdictional Challenges to Policy and Management

Scientific advances in forecasting species spread are increasingly employed in management, especially within single political jurisdictions. However, ecosystems under invasion are often shared by multiple political jurisdictions, a situation that often leads to suboptimal risk management. First, the weakest link problem exists where one jurisdiction has greater invasion risk tolerance than a neighboring jurisdiction; an invasion will likely start in or spread from the jurisdiction with the greater risk tolerance (102). Second, one jurisdiction may spend less on prevention than is socially optimal if it does not account for the positive externalities associated with its spending on the welfare of the neighboring jurisdictions. Third, the cooperation required to achieve the social optimum may not occur when different jurisdictions make independent choices among alternative management strategies. Multijurisdictional management of invasive species is thus a vital but difficult frontier for bioeconomic research and application (102).

### 4.2. Emerging Research Questions Regarding Dispersal of Invasive Species

1. What will be the influence of changes in climate, trade patterns, and policies on invasive species spread and dispersal vectors (103)?
2. Could game theoretic research on management choices by neighboring jurisdictions and communication help overcome multijurisdictional challenges in risk management?

## 5. SURVEILLANCE FOR EARLY DETECTION

Surveillance is looking for invasive species to make management actions including eradication and control more effective and/or more efficient. Surveillance is often informed by analyses of other information, including the sorts of dispersal models described in the previous section. Early detection and eradication of invasive species requires surveillance of pathways and suitable habitat, just as cancer detection and eradication in human patients requires routine checkups (104). Historically, however, surveillance for terrestrial weeds, aquatic pests, and other invasive species depended on costly and often ineffective field surveys (105). As in medicine, cost savings from prevention are driving increased interest in building regional and national invasive species surveillance programs (106, 107). On the basis of recent advances, an ideal surveillance program includes the following:

- the identification of high-risk species (Section 3), high-risk pathways and routes of spread (Section 4), and suitable habitat (Section 6)
- sharing resources with other management programs, e.g., monitoring of native species or environmental quality metrics such as water quality (108)
- mobilizing citizen scientists, who can reliably identify and map species invasions and can be more cost effective than researchers in cases of easily identified invaders (109)
- involvement of multiple jurisdictions (102)
- employment of emerging tools and technologies that increase the speed, accuracy, and sensitivity of detection

Genetics-based surveillance using environmental DNA (eDNA) is now possible in terrestrial (110, 111) and aquatic (112) environments. Species surveillance using eDNA exploits the fact that the environment contains the genetic signature of its occupants, making it possible to sample DNA from rare taxa that are present but not detectable by traditional means in natural habitats (36) and pathways (e.g., ballast water) (113). Most recently, high-throughput sequencing of eDNA enables surveillance for all potentially invasive (as well as native) species, including those that are unexpected (114).

In both human cancer detection and invasive species surveillance, innovation and technology, e.g., use of drones and robots (115), have improved the sensitivity of detection and control. However, medicine also provides a cautionary note: False-positive detections (and even true-positive detections) can motivate unnecessary or ineffective treatments that make the cure more dangerous and/or more expensive than the disease. Similarly, early detection of invasive species is useful only if effective eradication or control tools exist and can be mobilized (19). Otherwise, the cost of gathering information is greater than its value (116). Better statistical estimates of false detection results (117, 118) and improved control technologies can decrease the occurrence of such outcomes. Thus, the decision to implement a surveillance program depends on the accuracy of detection and the availability of effective management actions.

The following are the emerging research questions regarding invasive species surveillance:

1. How can multiple emerging technologies, including genetic tools, remote sensing, and drones, be integrated into surveillance programs?
2. Which models of citizen science surveillance programs are most effective?
3. Which empirical, modeling, and statistical approaches can best improve estimates of error rates in emerging eDNA surveillance methods?

## 6. SPECIES DISTRIBUTION MODELING

Given surveillance tools and knowledge about where pathways are likely to deliver a species, the next challenge is to identify habitats where a potentially invasive species may establish viable populations, i.e., the species' potential distribution (119). Ecological niche theory holds that this

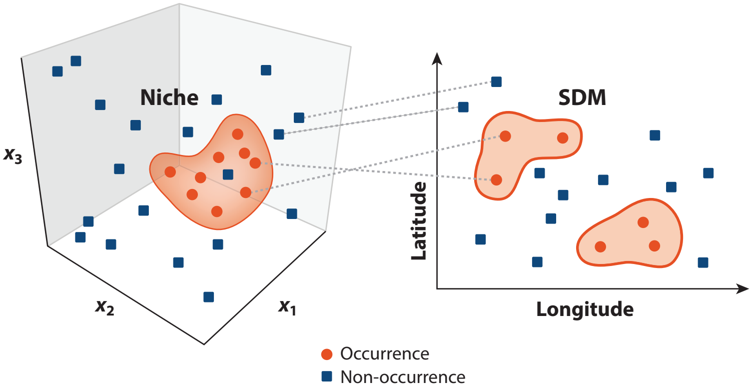

**Figure 4**

The ecological niche is designated by a boundary (*orange curved outline*) in the space of environmental variables separating records of occurrence (presence) from records of nonoccurrence (absence). Some environments belong to the niche despite the species' absence. Ecological niche modeling refers to the estimation of the boundary or a probability density from which that boundary can be constructed. Species distribution modeling (SDM), or mapping, projects the ecological niche model onto a geographic coordinate space. Although every point in geographic space exists in niche space, not all points in niche space are realized in nature, and some points in nature may be multiply realized in environmental space. Thus, these two spaces do not have a one-to-one relationship, but the relationship between these two spaces yields a useful approach to model estimation and mapping.

distribution is the projection of the ecological niche onto a landscape, where the environment at each point in the landscape has a set of values corresponding to various measurements (e.g., average annual temperature, average annual rainfall, soil type), and the niche is the relatively small set of environments in which the species may persist (**Figure 4**) (120, 121). Species distribution modeling (SDM) consists of (*a*) identifying relevant environmental covariates, (*b*) estimating a model of the boundary between niche and non-niche environments, and (*c*) applying the fitted model to environmental data for the area of interest. SDM is increasingly sophisticated and accurate (122). In some cases, reliable models may be fit to as few as 20 observations, if those points are sufficiently representative of the niche range (123).

Niche models may be based on underlying physiological processes and ensuing environmental tolerances as evaluated under laboratory conditions (124) or on statistical associations with observations in the field (122). Because the necessary information about physiology and life history is typically not available for most potential invaders, statistical models are most common and fall into two types. The probabilistic approach seeks to estimate the conditional probability of occurrence given the vector $x$ of environmental variables (122, 125, 126). That is, if $y$ is an indicator variable for the occurrence of a species at site $i$, one step in the niche modeling process is to estimate a model for the conditional probability $P(y = 1 \mid x) = f(x)$. The boundary of the potential niche is assigned to some threshold, e.g., $f(x) = 0.5$. In contrast, the boundary estimation approach seeks to identify the decision boundary directly (121, 127).

SDM is increasingly used in risk assessments of nonindigenous species in terrestrial (128), marine (129), and freshwater habitats (e.g., 130). If a probability model is fitted, the estimated suitability can be used to prioritize locations for surveillance and eradication (128, 131). Although some report an absolute probability of occurrence, relative suitability is more robust (132). In all cases, making predictions to new ranges can challenge model assumptions of stationarity

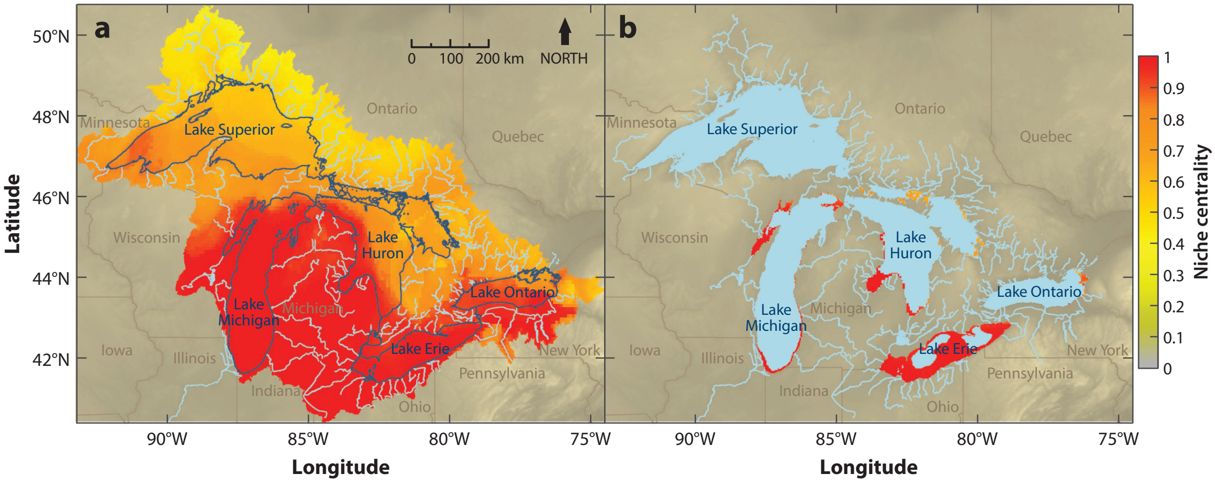

**Figure 5**

Relative suitability of Laurentian Great Lakes for northern snakehead as indicated by species distribution modeling. (*a*) The results were driven by occurrence data (192) (unique locations outside of the Great Lakes) and 19 global climatic variables, and (*b*) then restricted by habitat suitability (>18°C benthic temperature required for spawning) (A.M. Kramer, G. Annis, M.E. Wittmann, W.L. Chadderton, E.S. Rutherford, unpublished information). Thus the distribution estimated with climate data alone (*a*) overestimated the distribution relative to a distribution considering (*b*) available habitat within that climate envelope.

(122) and niche stability (133). The assumptions are violated because the geographic range of an invading species is, by definition, not at equilibrium, and niche shifts often occur during invasions (134). Current research is focusing on improved algorithms and applications (135, 136), as well as incorporating the effects of species interactions (137). Confidence in model outputs is improved by testing whether models are transferable to novel ranges (138, 139).

When applied carefully, the outputs of these models then offer a crucial visual tool for communicating risk to policy makers and managers. If a species is detected in a habitat but is unlikely to persist there, costly eradication efforts can be avoided. By contrast, prime habitat for establishment may justify both aggressive surveillance and eradication or control efforts. For example, in a recent binational Canadian-US ecological risk assessment for grass carp (*Ctenopharyngodon idella*) (140), comparison of maps from several SDM models (e.g., 141) suggested that four of the five Laurentian Great Lakes contain prime habitat, but the suitability of habitat in Lake Superior was uncertain. A global analysis revealed that relative suitability in niche models correlated with the population growth rate in established grass carp populations (142). This combination of information convinced managers of the desirability of preventive action. More recent efforts for grass carp and other species, such as northern snakehead (*Channa argus*) (**Figure 5**), incorporate additional habitat covariates, as described in the sidebar Refining Species Distribution Modeling with Higher-Resolution Habitat Data.

The following are the emerging research questions regarding SDM:

1. Which SDM methods best extrapolate to new ranges and are most robust to potential niche shifts?
2. How can new global databases of aquatic environmental covariates (145), which have previously been nonexistent at the global scale, be employed in SDM?

## REFINING SPECIES DISTRIBUTION MODELING WITH HIGHER-RESOLUTION HABITAT DATA

Northern snakehead (*Channa argus*), an East Asian fish, has established in several areas of North America and concern exists that its spread into the Laurentian Great Lakes would have negative impacts (143). A boundary estimation approach using native- and invaded-range occurrence records and global climate data estimated that large parts of the Great Lakes watershed are suitable for northern snakehead (**Figure 5**). Minimum temperature requirements for spawning (144) were used to identify the subset of species distribution modeling (SDM)-identified environments that would likely provide suitable habitat (**Figure 5**). Refinement of SDM output by higher-resolution habitat data (which is often available for only small areas) can guide surveillance and other management efforts for many species.

## 7. LINKING ECOLOGICAL AND ECONOMIC MODELS TO ESTIMATE IMPACTS ON ECOSYSTEM SERVICES

Even when natural resource managers know where a nonindigenous species might thrive and become invasive, they cannot wisely allocate resources to management actions without forecasts of the likely magnitude of damages. However, most scientific studies on the impact of invasive species focus on observations of current damage and not on prediction of future impacts (146). A vast literature demonstrates that ecological impacts are often large and widespread, affecting populations and communities of indigenous species and ecosystem processes in terrestrial, freshwater, and marine environments (3). In addition, a growing number of studies also estimate financial damages at large scales (147–149). On a species-specific level, assessments of currently existing large impacts are also common. For example, the American chestnut (*Castanea dentata*) was driven to functional extinction by pathogens over its entire range of 3.6 million hectares within 150 years (150). Many other tree species are now in slow-motion extinction owing to other introduced pests (151). In four of the five Laurentian Great Lakes, economically valuable lake trout (*Salvelinus namaycush*) were extirpated within 30 years of invasion by the parasite sea lamprey (*Petromyzon marinus*) (152). The ongoing invasion of *Dreissena* mussels (**Figure 2**), combined with low nutrient loads and the top-down effects of a large piscivore population, led to the collapse of Lake Huron's valuable salmonid fishery (153). Thus, both direct and indirect ecological impacts in all ecosystem types can have important economic consequences.

These studies—especially those focusing on financial damages—may motivate public and political interest in allocating resources to reducing damages, but they often use unsophisticated methods, produce highly uncertain damage estimates, and do not capture how damages would respond to management interventions. All current national- or multinational-scale financial damage assessments also ignore human responses to changing ecosystem services, which potentially mitigate damages (154). Studies with higher taxonomic, geographic, and temporal resolution and that include feedbacks within the economy are likely to be more useful in risk assessments intended to help guide choices among alternative policies (e.g., 155, 156). Such studies, including comprehensive process-based models to assess the direct and indirect environmental impacts of invasive species, are becoming more common as data accumulate on the impacts of invasive species, models of ecological systems become available, computational power increases, and demands grow for improved science-based management guidance (157). However, management-relevant economic assessment of direct and indirect impacts has lagged behind advances in environmental assessment.

Economic assessments have largely been organized around single economic sectors (often stakeholder groups) that are more readily identified with the initial stages of invasion. Thus, the focus has been on quantifying lost revenues or costs of treatment associated with an invasive species using methods referred to as partial budgeting. Economic uses, including nonmarket uses, of the natural resources directly impacted are documented, and production models are used to measure the impacts to crop yields, native species biomass, declines in economic efficiency, replacement costs, and the effects of diverting factors of production to control and prevention (158–161). To include broader environmental concerns, replacement and control costs are often used to assess nonmarket impacts. For example, Kovacs et al. (86) combine a spread model for the emerald ash borer with costs of treating, removing, and replacing trees within that footprint to calculate potential impact of the emerald ash borer. Partial budgeting is relatively easy to employ because it often focuses on impacts to an individual sector or firm (162), but it can be extended to impacts across multiple sectors and regional incomes with input-output models such as IMPLAN. Examples include assessments of the potential impact of foot-and-mouth disease in Kansas (163), yellow star thistle in the rangelands of Idaho (164), and invasive plants in Florida (165).

Partial budgeting approaches have the advantage of being easily understood by stakeholders, but economists recognize that such valuation measures exclude human behavioral changes in response to environmental changes, which are typically large and economically important. Human behavioral response in turn requires a specification of how humans behave and interact in markets. A challenge then for more assessments including human adaptation is choosing which markets to include. Economists have taken two approaches that represent a continuum of increasing comprehensiveness beyond partial budgeting.

First, partial equilibrium models introduce economic behavior and market impacts for a single industry. Generally, invasive species cause shifts in some measure of environmental quality that in turn affects supply or demand curves of a single related economic good or service. The change in environmental quality leads to a new equilibrium price and quantity of the related good. The impact of the invasive species is then calculated as a change in market welfare on the basis of changes in price and quantity. Such models have been used to assess the impacts of banning apple imports into Australia (166), quarantines to prevent spread of disease (160), and calculating the optimal amount of plant inspections to prevent introduction of exotic pests and diseases (167). Finnoff et al. (168) investigate the relationship between risk preferences of firm managers and relative investments in prevention and control. Haight & Polasky (169) investigate firm behavior when the level of invasion is uncertain either because of imperfect monitoring or a delay in detection. Partial equilibrium analysis is appropriate when impacts are limited to a single sector of the economy and when the income effects are likely to be small. These conditions hold during the early stages of an invasion.

Second, general equilibrium models extend consideration of the impacts across many industries in an economy. All regional prices, incomes, and flows of goods, services, labor, capital, and developed natural resources are determined within the model (170). This is in contrast to partial budgeting and partial equilibrium approaches, which ignore many key economic responses and hold most economy-wide prices constant. The welfare estimate generated by a general equilibrium model considers the economy-wide impact, overcoming the serious biases in welfare estimates that can result from partial budgeting and partial equilibrium approaches (171–173).

Although equilibrium models are large improvements over earlier economic modeling, most studies still treat the economic system as static and unresponsive to invasion. This does not reflect reality for large-scale invasions when human behavior, and thus economic systems, responds to the effects of invasive species and can be as dynamic as ecological systems (174). A

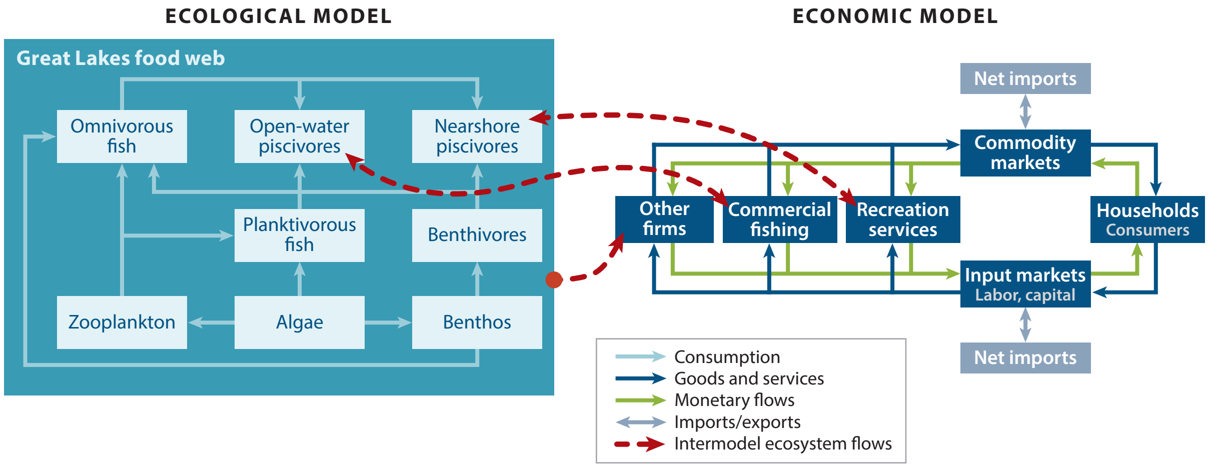

**Figure 6**

(*left*) A model of a Laurentian Great Lakes food web linked to (*right*) a computable general equilibrium model of the regional economy by recreationally harvested fish species, commercially harvested fish species, and raw water use by energy producers, other industries, and municipalities. In the linked model, outputs of each model are inputs to the other model.

recent bioeconomic approach overcoming this limitation dynamically links the forecasts from comprehensive ecological process models of responses to invasive species with a multimarket general equilibrium model (**Figure 6**). Current examples sacrifice spatial detail to provide a consistent framework for assessing the economic impacts of invasions across multiple sectors of the economy and a more complete accounting of ecological and economic effects on ecosystem services (157, 175). As described in the sidebar Ecological-Economic Feedbacks During Invasion, a linked model identified the impacts of potential invasion by silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*) into the Laurentian Great Lakes, and quantified the bias in predictions if feedbacks between the ecological and economic systems were ignored.

To incorporate the spatial dynamics that are important in ecosystems and human markets, which are not captured by the procedures described above, another emerging approach in bioeconomic research uses geographic information systems (GIS). In this approach, GIS link impacts

## ECOLOGICAL-ECONOMIC FEEDBACKS DURING INVASION

Bighead carp and silver carp are planktivorous fish native to Asia that were introduced to catfish farms in the United States in the 1970s; the carp escaped and spread rapidly. A food web model suggested that if Asian carp invade Lake Erie, walleye (*Sander vitreus*) and rainbow trout (*Oncorhynchus mykiss*) would decline, whereas smallmouth bass (*Micropterus dolomieu*) and yellow perch (*Perca flavescens*) would increase (176). By contrast, when the food web model was linked to an economic model (J.L. Apriesnig, T. Warziniack, D.C. Finnoff, K.D. Lee, M.E. Wittmann, H. Zhang, unpublished information), the feedbacks between the food web and human behavior changed the forecast biomass for walleye and yellow perch in different directions (see **Supplemental Figure 1**). The differences were driven by contrasting changes in exploitation rates in the US fisheries for walleye, which is tightly regulated, and yellow perch, which is less tightly regulated. Thus, ignoring the reciprocal interactions between ecological and economic systems could lead to incorrect forecasts and inefficient management choices.

Supplemental Material

to multiple ecosystem services across landscapes and provide a common framework for analysis among natural and social scientists. The InVEST (Integrated Valuation of Ecosystem Services) and ARIES (Artificial Intelligence for Ecosystem Services) models combine ecological production functions with economic valuation methods in spatially explicit models for ecosystem services (177, 178). In such models, a parcel of land has the ability, for example, to provide wildlife, sequester carbon, house humans, or grow crops. An application of InVEST, for example, showed that Minnesota land devoted to agriculture yields higher financial returns to landowners but yields lower social returns because of reduced carbon sequestration, less wildlife habitat, and impaired water quality (179). These spatially explicit tools have not yet been used extensively to address invasive species impacts and benefits of management.

As the literature reviewed above illustrates, models combining ecological and economic analyses are capturing more of the feedbacks known to be important, but current limitations have important consequences for knowledge and management (180). Models now in use still focus primarily on connections between several parts of the ecosystem with little connection to the economic system (water flows, biodiversity, carbon sequestration) (e.g., 176) or on connections between several parts of the economic system with limited connections to the ecosystem (for example, models where primary impacts of invasive species are on fisheries) (171–173). Furthermore, important spatial aspects are rarely included. The current investigations result partly from stakeholder-driven impact studies [e.g., most of the estimates in reports by the Congressional Office of Technology and Assessment focus on impacts to a single economic sector, with agriculture featured prominently (181)] and partly from the tendency for interdisciplinary research to focus on a particular element of the natural world (e.g., aquatic invasive species impacts on aquatic ecosystems). Given the current research landscape, the only way to achieve a broad understanding of the impacts for a particular invasive species is to draw from several disparately directed studies. If researchers' models incorporated broader ecosystem service and landscape perspectives, managers would have more useful guidance.

The following are emerging research questions regarding bioeconomic impact assessment:

1. Can bioeconomic models that simultaneously include dynamic feedbacks within the ecosystem, within the economy, and between the ecosystem and the economy (including human adaptation) be implemented and communicated quickly and simply enough to provide reliable management guidance?
2. Can spatially explicit approaches to guide invasive species management incorporate bioeconomic equilibrium methods to provide reliable management guidance?

## 8. BENEFITS OF COMPREHENSIVE RISK ANALYSIS

Although risk assessments of one transition probability can often inform a management decision about one stage of invasion, integrating multiple approaches across the invasion process likely represents the most effective management strategy when the opportunity exists (**Figure 1**). Policy and management of ships' ballast water is an instructive example. Risk assessments of species and pathways identified ships' ballast water as a global pathway with a high probability for species introductions (182) and for spread following introduction (82). Therefore, this became one of the first pathways to get global policy treatment (see Section 3). In various parts of the world, including the Laurentian Great Lakes, managers identified ballast-mediated species of particular concern (see Section 3), identified and modeled the likelihood of dispersal by secondary pathways (see Section 4), employed advanced genetic tools for surveillance in the environment and to screen for high-risk species in ballast water (Section 5), developed species distribution modeling to

## ECOSYSTEM SERVICE BENEFITS FROM LARGE-SCALE ERADICATION AND CONTROL PROGRAMS

Large-scale tests are underway on the selectivity and efficacy against dreissenid mussels of a newly developed toxin (183). A coupled ecological and economic model (see section 8) revealed that substantial ecosystem services would accrue to recreational anglers if dreissenid mussels were controlled in either Lake Michigan or Lake Erie (**Figure 7**). The magnitude of benefits depends on the intensity of treatment, reflecting the complex ecological interactions between dreissenid mussels and a complex portfolio of species and ecosystem services. For Lake Erie, a 50% reduction in mussels produced the largest welfare gain, driven by the increased abundance and harvest of fish including rainbow trout and walleye. A 99% dreissenid reduction resulted in a small welfare loss as reductions in smallmouth bass, lake trout, and lake whitefish (*Coregonus clupeaformis*) overwhelmed increases in other species. For Lake Michigan, the greatest welfare gain resulted from the greatest reduction (99%) of mussels because increases in salmonid abundance and harvest tracked the decline of dreissenid mussels (**Figure 7**). These results illustrate the usefulness of a coupled ecological-economic modeling framework to evaluate management scenarios, especially when complex interactions can produce surprising outcomes.

predict where the probability of suitable habitat was greatest (Section 6), and estimated the probability of economic consequences of ballast-mediated species (156). The large and still growing and spreading losses from ballast-mediated species like dreissenid mussels (**Figure 2**) is driving increased interest in control research and development. As described in the sidebar Ecosystem Service Benefits from Large-Scale Eradication and Control Programs, new control technologies may bring substantial benefits.

Comprehensive risk analysis strategies like those employed for ballast water are needed for both aquatic and terrestrial invasive species, including forecasts of initial arrival at airports and seaports, subsequent dispersal, and management options to reduce the transition probability at

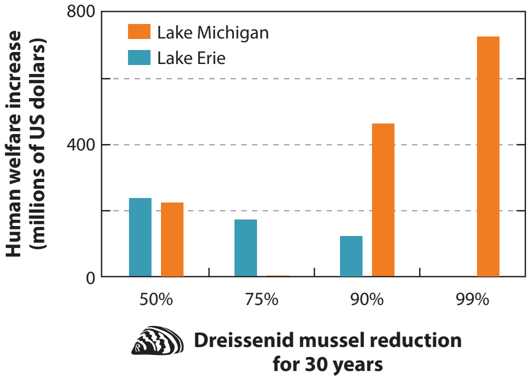

**Figure 7**

Increases in human welfare (in millions of US dollars), presented as aggregate willingness to pay, as measured by the net present value of income that households were willing to forgo to experience the benefits resulting from a simulated control treatment to reduce dreissenid mussels by different percentages over 30 years (M.A. Barnes, unpublished information).

### RISK MANAGEMENT OF AN AQUATIC PLANT

*Hydrilla verticillata* is one of the most damaging freshwater invaders in the southern United States (187). Following one of the northernmost invasions by this species in North America (Lake Manitou, Indiana), the Indiana Department of Natural Resources launched a risk management strategy involving surveillance and eradication. Based in part on previous and ongoing scientific studies of transport and desiccation tolerance (185), the Indiana Department of Natural Resources searched public access lakes within a 100-km surveillance radius of Lake Manitou for three consecutive years following the initial discovery in 2006, and no other lakes were found to contain the plant (D. Keller, Indiana Department of Natural Resources, unpublished data). Herbicide applications and monitoring have continued annually. In 2014, no *Hydrilla* was detected. Boat quarantine and other management actions have now ceased as a result of this important science-based success in invasive species management.

each invasion step (**Figure 1**). For example, modeling the movement of infested wood to prevent the spread of terrestrial wood-boring plant pests (184) and the movement of recreational boaters to prevent the spread of aquatic plants are conceptually similar (95). In both cases, gravity models can forecast potential routes and ecosystems at highest risk (78, 93). More detailed understanding of the biology of organisms is often needed to refine forecasts. For the overland transport of aquatic plants on trailered boats, for example, understanding a species' life history, knowing the response to desiccation stress in transit (185), and identifying suitable habitat (e.g., with SDM) are all essential components of a comprehensive risk assessment and management strategy (97, 186), as described in the sidebar Risk Management of an Aquatic Plant.

## 8.1. More Control Technologies Are Needed

If the costs and side effects of eradication and control technologies for more taxonomic groups can become sufficiently low to be both financially feasible and environmentally acceptable, control of invasive species could deliver large net ecosystem service benefits. Large-scale eradication or control programs for invasive species are increasingly common and successful, driven by increasing damage from invasions, more effective methods, and new technologies (19, 188, 189). Research and development for new selective control technologies against many different taxa are needed, potentially including new genetic approaches, e.g., gene drives (190, 191). Improved surveillance technologies make eradication and control technologies more effective because such efforts are more likely to be successful when populations are discovered while they are small, leading to successful management. A virtuous cycle of research and development is needed to protect ecosystem services from invasive species and increase net benefits to society.

## 8.2. Emerging Research Questions Regarding Comprehensive Risk Management

1. What new methods and tools might be effective for eradication and control, and what are their potential side effects?
2. How can alternative comprehensive management scenarios be produced more quickly and cheaply to inform decision makers?

## 9. QUANTIFYING AND COMMUNICATING UNCERTAINTY

Because of research advances, all the transition probabilities associated with an invasion (see Section 1, **Figure 1**) are now estimated with increased accuracy. However, uncertainty—often large uncertainty—remains a characteristic of estimates of the transition probabilities and of all the other parameters of risk analysis discussed above (e.g., estimates of financial costs and benefits) (192). The public and policy makers often perceive uncertainty as a shortcoming of scientific results. Scientists, by contrast, often see uncertainty as a characteristic to be quantified and considered in decisions but often fail to successfully communicate this perspective (193). Specific sources of uncertainty in both biological and economic models include process uncertainty, model uncertainty, observation error, and limited data availability (194). If uncertainty is ignored or not communicated, management actions are unlikely to be commensurate with invasion risks. At least four approaches have been used to incorporate uncertainty into invasive species forecasting.

First, the use of multiple independent models or techniques to forecast species invasions can delineate key uncertainties. In the use of species distribution models, different input data, modeling techniques, and spatial resolutions can produce multiple differing range forecasts for a single species. Managers may choose to consider the similarities and also the differences of multiple models to estimate the risk and confidence in predictions (140). Including uncertainty helps decision makers weigh the potential risks posed by a biological invasion (e.g., species impacts) against the risks associated with management actions (e.g., impacts to nontarget organisms). Although the decision to invest in prevention or control for an invasive species remains complex, the ability to understand how much uncertainty may exist improves the ability of the natural resource manager to make wise decisions (195).

Second, in cases where there are significant gaps in empirical evidence or disagreements, expert elicitation methods are available to characterize that uncertainty (196). Perhaps most useful are quantitative techniques, such as structured expert judgment (SEJ), that involve empirical validation of expert assessments and generate explicit uncertainty ranges for variables of interest (197). SEJ has been used to assess invasive species impacts to ecosystem services, ranking damages relative to both their magnitude and level of uncertainty (156). Similarly, SEJ was employed to forecast ecological damages prior to invasion (198). In both examples, key uncertainties were quantified, providing a foundation for future research paths to reduce these uncertainties. Since the publication of a study to quantify the uncertainties associated with 17 different Asian carp prevention strategies (199), multiple field and laboratory experiments have been published (200–204) that directly address the uncertainties presented in Wittmann et al. (199).

Third, addressing uncertainty can increase stakeholder engagement and incorporation of adaptive management strategies that allow for continued learning (205). Incorporating uncertainties into decision making increases transparency, and resource managers who effectively communicate this process may face less public backlash than those who try to remove uncertainty from decision making (206).

Finally, by integrating feedbacks between ecological and economic systems as highlighted in the previous two sections, researchers have been able to identify overlapping ecological and economic uncertainties and suggest policies to leverage this insight (180).

### 9.1. Robust Management Under Uncertainty Favors Prevention Over Later Management

Forecasts of the impact of an invasion (or of multiple invasions from a transportation pathway) are often fraught with uncertainty. Uncertainty is propagated as more invasion stages are included in such comprehensive risk assessments, such as some of those described in Sections 7 and 8. If uncertainties are great, a shift from trying to identify the single optimal quantitative management strategy may be necessary. Instead identifying management alternatives that are robust to uncertainty often becomes the goal (207). Robust strategies can bring net benefits under a range of future scenarios and are therefore often less susceptible to failure than a management alternative that is selected because it is optimal under what is thought to be the single most likely future realization (i.e., inadequately considering the uncertainty in forecasts). Considering the process of invasions and the management options at each stage of invasion (**Figure 1**), the overall most reliably beneficial and robust strategy for an invasion that has not happened (or for a vector that may deliver many species in future) is likely to be a strategy that addresses the earliest stages of invasion, especially those activities that emphasize prevention. At this stage of invasion, uncertainties in risk assessment have not propagated, and many management strategies are likely to be highly effective against a wide variety of species entrained in a single pathway.

### 9.2. Emerging Issues Regarding Uncertainty in Risk Assessment and Management

1. What combinations of expert elicitation, process modeling, scenario building, and robustness theory are most helpful to guide management?
2. What are the most effective ways to communicate uncertainty at the interfaces among scientists, policy makers, managers, and the public?

## 10. CONCLUSIONS

For the pharmaceutical supply chain, the food supply chain, and infectious disease outbreaks, the large costs of do-nothing management gave way long ago to policies based on risk analysis, which delivered large benefits to society. Likewise, as illustrated in the sections above, a risk analysis approach has improved the estimation of each of the transition probabilities (and their uncertainties) involved in biological invasions and has facilitated bioeconomic analyses of the costs and benefits of alternative management approaches. Recent advances in biological and economic risk analysis on invasions have informed—and in many cases prompted—improved international and national policies and management regimes for each stage in the invasion process (**Figure 1**). Many more improvements are possible if recent research results are adopted by more political jurisdictions and if further investments are made in research and technology to improve invasive species forecasts and increase the variety and effectiveness of management options.

As reviewed above, science-based risk management programs exist now that were impossible a decade ago (**Figure 1**). Screening programs to keep invasive species out of commerce while maintaining commerce in benign species exist, but many more are needed for different taxa and ecosystems. Management practices to reduce species in ships' ballast water are improved but require more rigorous evaluation and extension to biofouling on ships, as well as extension to other intercontinental and intracontinental pathways. Improved surveillance programs for early detection of incipient invasions rely on citizen science, new eDNA technology, drones, and remote sensing—all areas ripe for rapid progress if additional investments are made. Many of these risk management options are now more efficiently deployed geographically because of improvements in spatial modeling of pathways and suitable habitat for invaders. Continuous improvement and application of pathway and habitat modeling are likely to bring greater societal benefits. Finally, as reviewed above and emphasized by other recent theoretical and empirical studies (23, 168, 208), ecological and bioeconomic analyses have demonstrated that greater investments in prevention and other management activities early in the invasion process almost always bring net benefits. Increased cross disciplinary training in ecology and economics to increase research capacity in bioeconomics, and coproduction of research with decision makers (209), would enable more widespread management improvements.

Many of the advances reviewed here would have been impossible without recent improvements in data availability, increased computing power, and improved algorithms. Data availability is increasing for species distributions; species traits; movements of planes, ships, and other vectors; and ecological and economic models. Increased computing power and improved algorithms have been essential for pathway modeling, SDM, bioinformatics pipelines used in DNA-based surveillance, and linking ecological and economic models to create scenarios and simulations of management alternatives. However, without targeted investments in improving data availability, including in developing nations that are increasingly involved in the global trade network, the full benefits of improved risk management will not be realized even in the developed world.

Because species that cannot be located cannot be effectively managed, advances in surveillance are motivating renewed interest in research and development of eradication and control technologies. Synergistic leaps in effectiveness of prevention are possible with the simultaneous development of refined surveillance tools and new eradication and control tools that are both cost effective and have acceptable low nontarget effects in natural ecosystems.

Many of the recently developed risk assessment tools described here need periodic updating because so many ecosystems are subject to simultaneous changes in climate and other anthropogenic influences. It has been appreciated for many years that invasions themselves may cause changes in forecasts for the success and impact of subsequent invaders but that likelihood is now compounded by changing climate. These and other sources of uncertainty increase the value of management choices that are robust to uncertainty. Thus, prevention becomes the most cost-effective management response with respect to potential future invasions. This is especially true for management of transportation pathways, where a single prevention practice may simultaneously prevent the invasion of many species.

## SUMMARY POINTS

1. International and national policies governing invasive species increasingly mandate risk analysis, partly in response to research-driven improvements in risk analysis.
2. Species-specific trait-based risk assessments estimate multiple transition probabilities (establishment, spread, and impact) for diverse taxa with increasing accuracy; their use in management produces large environmental and net economic benefits for commerce in living organism pathways.
3. Spatially explicit models estimate the probability of dispersal with increasing accuracy and improve management efficiency by guiding spatial prioritization for management, especially for transportation pathways.
4. New information-gathering methods including surveillance technologies and approaches (e.g., eDNA, remote sensing, drones, citizen science) make early detection of invasions more likely; additional eradication and control tools would increase the value of this information.
5. New SDM tools estimate the probability of invasive establishment with increasing accuracy, especially when combined with local habitat data; combined with dispersal models, they enable improved geographic priority setting for surveillance and control.

6. Ecological and economic systems are dynamic, and feedbacks within and between them can dramatically alter responses to management interventions. Thus, in the face of an invasion by Asian carps in Lake Erie, expected outcomes reverse for native Lake Erie fisheries, depending on whether feedbacks exist between the ecological and economic model systems.
7. Although bioeconomic risk analyses of invasions have become more common, it remains unclear which of the diverse modeling approaches that have been used are the most useful to specific management situations. In the research arena, a potential direction is to combine approaches, e.g., models that include multiple invasion transition probabilities in a general equilibrium economic model linked dynamically to an ecological model, all in a spatially explicit and dynamic framework.
8. Consideration of the typically large uncertainty around estimates of transition probabilities and economic parameters supports the conclusion that prevention is usually the most robust management option and the option most likely to produce the largest net long-term benefits.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review. The findings, views, and conclusions expressed in this article are those of the authors and do not necessarily represent the views of, and should not be attributed to, the National Invasive Species Council, the USFWS, the US Forest Service, or any other US government agency.

## ACKNOWLEDGMENTS

Grants from the US National Oceanic and Atmospheric Administration's (NOAA's) Center for Sponsored Coastal Ocean Research and from the US Environmental Protection Agency's Great Lakes Restoration Initiative supported research by many of the authors of this review. Other grant support came from the Great Lakes Protection Fund, the Great Lakes Fisheries Trust, the USFWS, the US Department of Defense's Strategic Environmental Research and Development Program, and the National Science Foundation's Coastal SEES program. Kristina Davis prepared most of the figures. We thank Pam Schofield and Amy Benson (US Geological Survey) for supplying the data for **Figure 2** and Raisa Beletsky (University of Michigan) for help with larval transport modeling. For helping to guide the research of many authors, we thank the NOAA Center for Sponsored Coastal Ocean Research–sponsored Bioeconomic Forecasting Management Transition Board, consisting of representatives of US and Canadian government agency representatives. This is a product of the University of Notre Dame Environmental Change Initiative and is NOAA Great Lakes Environmental Research Laboratory contribution number 1824.

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**Annual Review of Environment and Resources**

Volume 41, 2016

# Contents

## I. Integrative Themes and Emerging Concerns

## II. Earth's Life Support Systems

## III. Human Use of the Environment and Resources

## IV. Management and Governance of Resources and Environment

## V. Methods and Indicators

## Indexes

## Errata

An online log of corrections to *Annual Review of Environment and Resources* articles may be found at http://www.annualreviews.org/errata/environ