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Predicting Invasions of Nonindigenous Plants and Plant Pests

Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States, National Research Council

ISBN: 0-309-50914-9, 198 pages, 6x9, (2002)

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PREDICTING INVASIONS OF
NONINDIGENOUS PLANTS AND PLANT PESTS

Committee on the Scientific Basis for Predicting the Invasive Potential
of Nonindigenous Plants and Plant Pests in the United States

Board on Agriculture and Natural Resources
Board on Life Sciences
Division on Earth and Life Studies
National Research Council

NATIONAL ACADEMY PRESS
Washington, D.C.

NATIONAL ACADEMY PRESS · 2101 Constitution Avenue, NW · Washington, D.C. 20418

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This study was supported by Grant No. 00-8100-0518-GR from the U.S. Department of Agriculture's Animal and Plant Health Inspection Service (APHIS), Plant Protection and Quarantine. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the views of the organizations or agencies that provided support for the project.

Library of Congress Cataloging-in-Publication Data

Predicting invasions of nonindigenous plants and plant pests.
p. cm.
"Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States."
Includes bibliographical references and index.
ISBN 0-309-08264-1 (hardcover)
1. Nonindigenous pests—Control—United States. 2. Invasive plants—Control—United States. 3. Biological invasions—United States—Prevention. 4. Plant invasions—United States—Prevention. I. National Academy Press (U.S.) II. National Research Council. Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States.
SB990.5.U6 P74 2002
632'.5—dc21
2002003344

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Cover: Clockwise, from top left: Larvae of Asian long-horned beetle (*Anoplophora glabripennis*) in wood, USDA Forest Service. Dead American chesnut (*Castanea dentata*), spores of fungus *Cryphonectria parasitica* in background, William MacDonald, West Virginia University. Hemlock woolly adelgid (*Adelges tsugae* Annand), Kathleen Shields, USDA Forest Service. Fountain grass (*Pennisetum setaceum*), Richard Mack, Washington State University.

Printed in the United States of America

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Acknowledgments

This report is the product of many individuals. This report has been reviewed in draft form by individuals chosen for their diverse perspectives and technical expertise, in accordance with procedures approved by the NRC's Report Review Committee. The purpose of this independent review is to provide candid and critical comments that will assist the institution in making its published report as sound as possible and to ensure that the report meets institutional standards for objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the deliberative process. We wish to thank the following individuals for their review of this report:

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Although the reviewers listed above have provided many constructive comments and suggestions, they were not asked to endorse the conclusions or recommendations nor did they see the final draft of the report before its release. Dr. W.R. Gomes of the University of California oversaw the review of this report. Appointed by the National Research Council, Dr. Gomes was responsible for making certain that an independent examination of this report was carried out in accordance with institutional procedures and that all review comments were carefully considered. Responsibility for the final content of this report rests entirely with the authoring committee and the institution.

Finally, we would like to thank the staff for this project, including Robin Schoen, Study Director, Lucyna Kurtyka, Staff Officer, Karen Imhof, Project Assistant, and Norman Grossblatt, Editor.

Preface

As the United States faces biological warfare for the first time and ponders the consequences of growing genetically modified crops, a largely unnoticed biological attack is underway; actually, it has been under way for centuries and shows no signs of slowing. Nonindigenous species—animals, plants, and microorganisms occurring beyond their original geographic ranges—are flowing into this country at a remarkable rate. Often unchecked by natural enemies or forces that modulate their numbers, many of these will become invasive pests that threaten human, animal, and plant health. America's plant resources have been most affected, as foreign plants, arthropods, and plant pathogens attack our crops, gardens, urban treescapes, pastures, rangelands, natural forests, wetlands, prairies, and deserts. From coast to coast, there is hardly a place in the country untouched by invasive nonindigenous species.

In 1999, President Clinton established the National Invasive Species Council, which is composed of the heads of eight federal agencies, to develop a coordinated plan for managing nonindigenous invasive species. By one estimate, the toll of these species in lost crops and the cost of containment measures such as mechanical destruction, and the use of pesticides and biological control—is $137 billion per year. The indirect and ecological costs of losing native species because of attacks by or competition with invasive species may be incalculable. Moreover, while farmers, as caretakers of agricultural lands, have taken action to control pests in their fields, invasions into natural ecosystems have received far less attention; in many cases, there is little attempt to stop what some environmentalists describe as the "biological pollution" devastating our natural areas.

As a result, current estimates of the present and future costs of invasive species are almost certainly low.

The processes that facilitate the damage caused by invasive plants and plant pests once they are here are not well understood, but there is consensus that the increased rate at which these species are being introduced into the United States is the result of growth in trade with other countries and growth in worldwide tourism and travel. The sheer magnitude of those activities makes it virtually impossible to implement adequate systems for detecting known, unwanted plant pests as they arrive in cargo or with passengers at U.S. ports and move across borders. For example, the desire of gardeners and plant-lovers for "exotic" plants has fueled an influx, via mail and other import routes, of the seeds and cuttings of nonindigenous plants whose potential for invasiveness is unmonitored.

As the first line of defense against the entry of harmful nonindigenous species, the Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) faces an onerous task. The service is "to facilitate exports, imports, and interstate commerce in agricultural products and other commodities that pose a risk of harboring plant pests or noxious weeds in ways that will reduce, to the extent practicable, as determined by the Secretary, the risk of dissemination of plant pests or noxious weeds." APHIS must operate, therefore, in an environment of competing priorities—one to facilitate trade and the other to protect plant life from the adverse byproducts of trade. Supporters of each of those priorities—for example, importers of foreign produce versus domestic growers or the landscape industry versus the stewards of national parks—place APHIS practices and decisions under close scrutiny.

With resources to conduct spot checks of less than 2% of all incoming shipments at borders, air, and seaports, APHIS cannot reasonably rely on detection to screen out known nonindigenous species that are "hitchhiking" on imports. It must therefore estimate the economic and environmental risks associated with allowing the entry of a foreign commodity or crop. On the basis of such estimates, APHIS has the authority to prohibit imports, but not without yet another hurdle. Its decisions are bound by international trade law to be supported by scientific evidence. Thus, erecting a science-based system to identify potentially harmful nonindigenous plants, pathogens and arthropods has arisen from both national and international mandates. But that requirement places a heavy burden on our current knowledge of organisms and their potential behavior in a novel environment. Of all the factors considered when estimating risk, behavior in a new environment is the one for which the least information is available.

The National Research Council established the Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States in response to a request from APHIS to evaluate the state of scientific knowledge about biological invasions and the state of our ability to reliably predict the outcome of an accidental or intentional introduction of a nonindigenous species. Such information is important to APHIS as it makes regulatory decisions, and it is critical for our understanding of the behavior of harmful invasive species and of how we might curb their expansion and impact.

The committee was given the charge to

- Consider the historical record of weed, pathogen, and arthropod invaders, including pathways of their introduction
- Identify and analyze circumstances that could allow nonindigenous species to become invaders, considering the biotic and abiotic characteristics of potentially affected ecosystems, including agricultural systems, and the characteristics of nonindigenous plants and pests of plants that contribute to their potential invasiveness
- Determine the extent to which scientific principles and procedures can characterize the invasive potential of nonindigenous pests of plants and the degree of uncertainty intrinsic in such characterizations
- Identify research that could improve the prediction of invasiveness

This report summarizes the results of the committee's investigations. Our study was driven by the need to clarify the boundaries of current scientific knowledge and to guide the direction of our national effort to address the future introduction of harmful nonindigenous species.

Richard N. Mack, *Chair*,
Committee on the Scientific Basis for Predicting
the Invasive Potential of Nonindigenous Plants
and Plant Pests in the United States

Contents

PREDICTING INVASIONS OF
NONINDIGENOUS
PLANTS AND PLANT PESTS

Executive Summary

Biological invasions of nonindigenous plant pests—plants, pathogens, and arthropods—are serious threats to the rural, urban, and natural ecosystems of the United States. In the agricultural setting, hundreds of millions of dollars are spent each year on pesticides and herbicides to prevent native and nonindigenous pathogens, arthropods, and weeds from ruining crops. There are no treatments for some of them: the glassy winged sharpshooter that is spreading disease in California grapes, Karnal bunt in some wheat-producing states, citrus canker in Florida, and plum pox in Pennsylvania.

Suburban and urban areas have not been spared. The arrival of the Asian long-horned beetle has already led to the destruction of thousands of shade trees on the streets of Chicago and New York. Many suburban areas of the eastern United States have also been subjected to aerial spraying of insecticide to deter the southward spread of the European gypsy moth, which has defoliated thousands of trees in the region.

Equally threatened by nonindigenous plant pests are U.S. forests, wetlands, and other natural areas. Examples of these pests are the chestnut blight fungus (*Cryphonectria parasitica*), which all but eliminated the American chestnut from northeastern forests early in the 20th century; hemlock woolly adelgid (*Adelges tsugae* Annand) and balsam woolly adelgid (*A. piceae* Ratzeburg), which are killing native hemlock and fir, respectively, in the eastern United States; and the invasive plant *Melaleuca quinquenervia*, which has changed the hydrological characteristics and plant and animal life of the Everglades. The impact of invasive nonindigenous species on natural areas is likely to be permanent, in part because economic and environmental factors limit eradication or control options that may be appropriate in agricultural settings.

Only a small fraction of introductions of nonindigenous species result in invasions in the United States, but it is not obvious which nonindigenous plants, pathogens, and arthropods are benign and which will become important pests. Moreover, resources are not available to detect the introduction of every nonindigenous pathogen and arthropod or to monitor the fate of every imported plant, so alternative strategies to identify and eliminate pests are needed. The U.S. Department of Agriculture (USDA) asked the National Research Council's Board on Agriculture and Natural Resources (BANR) to examine what is known about nonindigenous plant pests so that it could be determined whether there is sufficient information to list the species that are potential invaders in the United States. To study the issue, BANR created the Committee on the Scientific Basis of Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States. The committee was charged to

- Consider the historical record of weed, pathogen, and arthropod invaders, including pathways of their introduction.
- Identify and analyze circumstances that could allow nonindigenous species to become invaders, considering the biotic and abiotic characteristics of potentially affected ecosystems, including agricultural systems, and the characteristics of nonindigenous plant pests that contribute to their potential invasiveness.
- Determine the extent to which scientific principles and procedures can characterize the invasive potential of nonindigenous plant pests and determine the degree of uncertainty intrinsic in such characterizations.
- Identify research that should be conducted to enhance the prediction of invasiveness.

The committee's study assesses the state of knowledge about biological invasions of nonindigenous plant pests, examines current capabilities to predict invasions and the identity or characteristics of invaders, and recommends ways to improve those capabilities. The committee was not charged with evaluating current government practices or suggesting policy; therefore, it has limited its comments on the regulatory activities and other functions of federal agencies to the extent to which they can or do contribute to the scientific basis of predicting the invasive potential of nonindigenous plants, pathogens, and arthropods.

PREDICTIBILITY OF THE INVASION PROCESS

Few arriving populations become established, even fewer populations of established nonindigenous organisms expand and spread dramatically, and the environmental and economic impacts of the ones that do spread vary widely. The events that take place during the transition between the phases of the invasion process are peculiar to each occurrence of a species' introduction, and biologists continue to seek patterns that could help to predict invasions. No known broad scientific principles govern "invasive potential" for all plant pests in all environmental circumstances. Many of the data from which such broad principles might be derived have not been collected.

However, much is known about the factors that contribute to invasions. Examining those factors provides descriptive information that can be used to *explain* what appears to be recurring in invasions. But to increase the *predictive* value of the factors, they need to be quantitatively evaluated in the context of different organisms in different conditions and as both independent and dependent variables. Elucidating the scientific principles that underlie invasions will not require a detailed understanding of the relationships among all organisms and their native and potential physical and biological environments. However, multiple approaches are needed to find a level of abstraction at which the predictive power of hypothetical outcomes is better than random. That level may be different for different groups of organisms or different environments.

Given the complexity of the dynamic systems involved in biological invasions, it is realistic to suggest that purposeful, long-term, broadly based research is needed to elucidate the underlying principles. Information that has already been collected on potential plant pests and on the events surrounding known invasions suggests that there are biological "leads" that could be followed to improve predictive capabilities. The committee's report examines those leads in substantial detail, and they are summarized here.

ARRIVAL OF PLANT PESTS

Historical data on the immigration of plants, arthropods, and plant pathogens suggest that introductions by natural means are uncommon; almost all introductions today are in some way facilitated by human activities. Arthropods and pathogens usually arrive in association with trade commodities. Additionally, a few hundred invertebrates and fungi have been intentionally released for the biological control of plant pests, and a small number of these have themselves become pests.

Accidental introductions of arthropods and pathogens are facilitated by these species' "hide and survive" attributes, such as small bodies, coloration similar to the carrying commodity, and concealment inside wood, roots, or buds. The ability to remain in a resting or resilient life stage substantially increases the species' chances of surviving transport. In that regard, the expansion of direct airline routes between foreign and U.S. cities has decreased travel time, enhanced the potential for survival, and increased the number of entry points for nonindigenous plant pests. Widespread use of containers in shipping has increased the difficulty of detecting pests.

There have been relatively few attempts to quantitatively evaluate the number, identity, and origin of arthropods, pathogens, and undesirable plants that inadvertently arrive at the borders and ports of the United States. Interceptions of organisms whose entry into the United States is restricted are documented in the Port Information Network (PIN) database maintained by the USDA Animal and Plant Health Inspection Service (APHIS) since 1985. Roughly 53,000 interceptions of arthropods, pathogens, and noxious plants are made each year by APHIS inspectors, who endeavor to examine up to 2% of the cargo, baggage, and related materials arriving in the United States. PIN data, however, have recognized limitations and have rarely been made available to scientists outside APHIS. Despite those limitations, the PIN database is a potentially valuable resource; collaborative efforts of APHIS officials and scientists in different disciplines to analyze the data could do much to enhance our understanding of the pathways by which potential invaders arrive in the United States.

In contrast with arthropods and pathogens, introductions of most nonindigenous plants into the United States are intentional. A minority of these species has become invasive, but there is no consistent effort to monitor the fate of plants that arrive. In addition to the demand for nonindigenous plants for landscaping and gardening, Internet-based sales and seed exchanges have encouraged importation. Although imported plants do not, as a group, share any syndrome of traits that enhance their ability to become invasive, some activities might favor the importation of plants that are likely to become established. For example, renewed interest in medicinal plants, such as herbs, has resulted in the importation of plants that are troublesome in parts of the United States. Likewise, there is an interest in plants for erosion control that are hardy and spread readily; these characteristics increase the chances that they will become invasive.

China is likely to be a source of new invasive plant pests because of the dramatic increase in trading activity between China and the United States, because the two countries share physical and climatic environments and many related plant species, and because many collectors and nurseries are particularly interested in plants from China.

ESTABLISHMENT OF PLANT PESTS

If nonindigenous plants, arthropods, and pathogens are introduced into a new environment in small numbers, they are not likely to survive, because of stochastic forces in the new locale. These forces are random demographic, environmental, catastrophic, and genetic events that can push small populations to extinction. The stochasticity can be overcome in some instances by factors that increase the chances that some members of a new population will survive; these factors include cultivation, the spatial distribution of the new immigrants, and multiple, sequential introductions that reinforce the size of the population and diversify the age distribution or genetic variability among its members. Information on such factors could be important in assessing the potential for establishment if it were possible to reliably quantify the effects of stochasticity on specific immigrant populations.

Abiotic forces (such as climate) and biotic forces (such as the availability of hosts, vectors, pollinators, or mutualists and the presence of competitors, predators, and pathogen antagonists) also affect the establishment of nonindigenous plants, arthropods, and pathogens. The life-history traits that equip particular species to deal with their environment are crucial in determining their survival.

Much of the quantitative information about the interaction between abiotic and biotic forces and the life-history traits that contribute to a species' establishment has come from monitoring the release of nonindigenous insects for biological control and from after-the-fact studies of species' invasions. Although research on a particular species or event can permit conclusions to be drawn about the combination of factors that lead to its survival or extinction, it has not been possible to generalize the findings to other events or other species. Little is known about the phenotypic plasticity of potential plant pests in different environments: we have scant knowledge of the range of tolerance of most plants, pathogens, and arthropods; and we have so little information about the stochasticity and amplitude of abiotic and biotic forces in any environment that reasonable predictions of the strength of their impact on a newcomer cannot be made.

Regardless of those limitations, key points have been identified. For example, climate, latitude, and the availability of a host appear to be among the primary determinants of the suitability of a habitat for insects. Consequently, insects from low latitudes might be less likely to become established in northern latitudes than the reverse, because these insects might find climatic conditions intolerable, fail to find a suitable host, enter diapause (a period of dormancy) too late in autumn, or break diapause too early in spring.

Other clues to the establishment by nonindigenous insects are found in research on diet breadth in insects, the temporal availability and spatial distribution of hosts, the similarity of potential invaders as the prey of predators in the new environment, and the diversity of the predator population. Establishment might also be associated with parthenogenesis, long-lived adult stages, high fecundity, and small bodies.

For pathogens, the availability of a genetically compatible host is critical. Knowledge of the regional distribution of pathogens and the frequency of different avirulence genes can be important in predicting the resistance or susceptibility of a plant taxon (that is, variety, race, subspecies, or genotype). If the virulence of a potential invading pathogen is known, the vulnerability of a plant taxon can be predicted rather accurately. Traits that appear to enhance establishment of plant pathogens are a short infection cycle, a high rate of production of infectious units, and a long infectious period.

The abiotic and biotic factors that affect the establishments of plants are less well understood. The most frequent biotic constraint on plants is attack by pathogens. Plants can have diverse characteristics that contribute to survival, such as the ability to propagate asexually and self-fertilize when the population is small; plants that outbreed when the population grows larger gain the benefits of genetic diversity in the long run. Traits associated with establishment include long flowering and fruiting periods that increase the chance of pollination and seed dispersal, a short juvenile period (the time from seed germination to the onset of flowering), high seed production, a capacity for seed dormancy and germination cuing, and the ability to use light efficiently.

In some plant groups, a combination of those traits has been shown to have predictive power in identifying invasive species, and these results should be useful in assessing new plant introductions in the taxonomic groups in question. It has not yet been possible to generalize the results across a broad taxonomic spectrum among vascular plants; moreover, there are exceptions (some invasive plants apparently have none of the traits, and some plants with the traits have not been shown to establish in a new range).

A key shortcoming of most studies that consider abiotic and biotic forces, as well as organisms' traits, is the lack of experimentally derived, explicit, quantitative data that would allow systematic analysis of the relative importance of factors.

TRANSITION TO INVASIVENESS

Experimental data related to a population's ability or inability to grow and spread once established are scant. It is possible to recognize an invading population and to speculate retrospectively on factors related to its success in the new range, but it has proved difficult to predict the success of a species in a given environment.

Many of the same species' traits and abiotic and biotic forces that affect a population's establishment continue to be important in its numerical and geographic expansion. Having reached a threshold size, an established population is much less subject to stochastic forces that could drive it to extinction, but the size and spread of the population are affected by the availability of and competition for resources and by mechanisms that facilitate dispersal.

Following in detail the movement of propagules (seeds, adult insects, eggs, spores, and so on) could provide useful information on whether some categories of potential plant pests might be more likely to become invasive than others. The spatial distribution of established populations that result from dispersal also probably plays an important role in their ability to become invasive. It is known that wind dispersal is more common in arid treeless ecosystems and that bird dispersal is more common in forest systems. Birds have often played a critical role in the spread of species with fleshy fruits. Consequently, nonindigenous species with fleshy fruits (and the pathogens associated with them) could as a group carry a high threat of spread and invasion.

There is no consensus as to whether a biologically diverse community is more or less likely to be invaded than one that is less diverse; there are theories but few experimental studies supporting each view. Obviously, a pathogen or arthropod faced with a monoculture of compatible host plants is in a good position to thrive, but many more nonindigenous pathogens or arthropods will have a better chance of finding hosts in a diverse community. It may also be more useful to focus on the concept of functional groups within a community, regardless of the taxonomic groups involved, or on resource availability and how variation in limiting resources might foster or hinder the invasion process.

Some clues to the ability of nonindigenous plants to become invasive are suggested by the traits by which some compete with native species or alter the new range to their advantage. Those traits include light-sequestering abilities (as in climbing vines), deep or dense root systems that capture water, abundant fruit or nectar that attracts pollinators, nitrogen-fixing capacity that alters soil composition, and fire-facilitating and fire-resisting attributes that alter fire cycles. Expression of any of these traits can greatly diminish the role of native species.

Genetic differentiation might be important in the long-term success of an established nonindigenous population in a new environment. The tempo of differentiation varies enormously among species, depending on how the organism uses sexual and asexual reproduction and on life-history characteristics. Multiple introductions and hybridization with native species are sources of genetic variation that can favor evolutionary diversification. As a result, novel genotypes that are locally adapted to conditions in the new range potentially can evolve. Modern agricultural practices can create selection pressures that shape plant pests that are specialized to the local crop environments. Selection pressures encountered during the invasion of natural habitats are even more complicated.

EVALUATING THE IMPACT OF INVASIONS

Predicting the consequences of invasions is challenging in invasion biology, in part because investigators disagree on how to measure the consequences. Invasions can be considered as having effects at five levels of biological organization: individual (including rates of growth, development, birth, death, and movement), genetic (including hybridization), population (mean and variance in abundance, population growth rates, and so on), community (species richness, diversity, and trophic structure), and ecosystem (primary or secondary productivity, hydrological characteristics, nutrient cycling, soil development, and disturbance frequency).

Furthermore, the influence of an invader can drastically affect the aesthetic value of an area. The loss in aesthetic value incurred when a biotic invasion occurs in a national park or national monument undercuts much of the rationale for the land's protection in the first place. There can also be cumulative and indirect effects of invasion by more than one nonindigenous species. The chief reason that the impacts of invasions are so difficult to evaluate stems from the lack of sufficiently detailed data on the species composition, structure, and function of ecosystems before they are invaded. Decades can pass between an introduction and the manifestation of its impact. As a result, we recognize that an invasion has occurred only after the ecosystem has changed. Before a predictive theory about the impact of a potentially invasive plant pest can be developed, better characterization of many more ecosystems in the United States is needed.

VALUE OF PREDICTIVE SYSTEMS

Methods or systems for predicting the invasive potential of introduced organisms have focused largely on identifying species that have a record of becoming invasive elsewhere and categorizing their invasiveness according to some schema. Expert judgment has been the most commonly used tool, and collective judgment can strengthen the reliability of such species' assessments. For example, an effort is under way to have members of an expert network rank wildland weeds in the United States against a list of invasiveness categories (Randall et al. 2001). The value of the proposed categories will be determined by the consistency of the experts' rankings.

Identification of potentially invasive species according to a suite of life-history traits (mostly in plants) has been attempted with some success. For a few taxonomic groups (woody plant species), the prediction of invasiveness on the basis of traits has been shown to be reliable and should be considered in the regulation of plant importation. Wider application of these approaches to other taxonomic groups has had mixed results.

Climatic simulation models (such as CLIMEX) that identify similar climates around the world offer a preliminary screening tool to evaluate the invasive potential of groups of organisms, based on comparisons of climates in a species' native and potential new ranges. The crucial limitation in using climate-matching as a predictor of establishment in a new range lies in the assumption that climate alone determines a species' distribution. Species' distributions are also strongly influenced by the biotic component of an environment.

Risk assessments conducted by APHIS for the purpose of regulating the importation of commodities or managing potential pests incorporate elements of a predictive system. The main limitations of these predictive elements are that they require subjective, qualitative determination of characteristics of nonindigenous species and the environments into which they might be introduced, and they identify risk by subjectively placing species and environment characteristics into likelihood categories. Thus, the manner in which these assessments are conducted reduces the opportunity for their replicability. Alternative methods that incorporate quantitative scenario analysis constitute an improved approach despite the lingering subjectivity in the probability distribution attached to events.

The weakness in prediction among current models of potential invasiveness and of risk assessments does not mean that they are unscientific. But a scientifically based predictive system for invasiveness should meet three criteria: it must be transparent, open to review and evaluation by experts; it must have a logical framework that includes independent factors identified through critical observation or experimentation, or both; and use of the framework must be repeatable and lead to the same outcome, regardless of who makes the predictions. Many of the systems of prediction, including risk assessments, do not always meet those criteria.

CONCLUSIONS AND RECOMMENDATIONS

After considering the history of invasions of plants and plant pests in the United States, reviewing scientific knowledge about the factors associated with invasive species, and examining efforts to predict the potential of species to invade, the committee reached the following four conclusions:

Conclusion 1. The record of a plant's invasiveness in other geographic areas is currently the most reliable predictor of its ability to establish and invade in the United States. The same is true for arthropods and pathogens if plants that they can use elsewhere occur in the United States.

Conclusion 2. There are currently no known broad scientific principles or reliable procedures for identifying the invasive potential of plants, plant pests, or biological control agents in new geographic ranges, but a conceptual basis exists for understanding invasions that could be developed into predictive principles.

Conclusion 3. The inability to predict accurately which nonindigenous species will become invasive stems from a lack of comprehensive knowledge of the events that dictate species' immigration (arrival), persistence (survival), and invasion (proliferation and spread) in new environments. The requisite knowledge would be based on critical observation of the natural history of nonindigenous species and experiments designed specifically to evaluate nonindigenous species in the stochastic environments they encounter in new ranges.

Conclusion 4. Some data on the natural history of plant pests exist, but they often reside in grey literature and in datasets that are not easily accessible. Data on events that potentially lead to invasions are frequently collected by federal or state agencies in the course of pest surveys and inspections and after releases of biological control agents. Such collections need to be more comprehensive and need to be implemented on a quantitative, statistically sound basis. Datasets need to be organized in a way that allows them to be analyzed and evaluated from the perspective of understanding invasiveness.

In the following recommendations, the committee points to ways of strengthening the scientific basis of predicting the invasive potential of plant pests. The first three recommendations are directed toward the regulatory activities of the U.S. Department of Agriculture (USDA)-Animal and Plant Health Inspection Service (APHIS) because they are related to our understanding of the scientific basis of prediction. The other recommendations require action by USDA, APHIS, other federal and state agencies, and the scientific community. Recommendations 4-7 are related to the documentation and standardization that is needed to understand invasions better. Recommendations 8-10 focus on needed research, and recommendations 11 and 12 point to the organizational infrastructure and scientific expertise that are needed to make headway against the problem of predicting invasions.

In the Committee's view, all of these recommendations carry a need for urgent implementation. The current basis for evaluating the potential risks by newly introduced nonindigenous species is not adequate to address the problem of biological invasions—a problem that is certain to continue growing in the coming decades.

USDA-APHIS ACTIVITIES

Recommendation 1. The Port Information Network (PIN) database maintained by APHIS is a potentially valuable source of information for understanding the pathways by which potential invaders arrive at U.S. borders, but the utility and availability of the data could be substantially improved. Sampling methodology should be statistically designed and implemented consistently. Sampling protocols at ports and borders should be re-evaluated and revised as necessary to ensure that pest interception data are accurate and meaningful. Data collection should be expanded to include vascular plants (in addition to those on federal lists of noxious weeds and seeds). Increased efforts are also needed to detect and identify pathogens consistently. Improved technology to detect hitchhiking insects and plant pathogens arriving with cargo, baggage, and related commodities could improve the utility of the PIN database (as well as reduce opportunities for new, potentially invasive pests to immigrate). The value of the database would be increased by including additional variables, such as a record of inspections that result in the detection of zero pests, some measure of the abundance of detected pests, and interceptions of nonquarantined pests. The data should be monitored consistently and regularly to identify and correct problems in data entry or maintenance. The PIN database should be accessible for analysis by investigators in universities and other agencies in collaboration with APHIS personnel who are familiar with the database.

Recommendation 2. APHIS risk assessments combine a system of predicting an organism's arrival and establishment with an estimation of the possible consequences. The assessments are based on scientific concepts but contain uncertainties because of gaps in available information. To strengthen the overall prediction of invasive potential, the basis of APHIS risk assessments should be better documented, and assumptions made in each step should be listed and explained, so that independent experts can rationally compare conclusions about the likelihood of arrival, establishment, and impact. The assessment procedure should be transparent, repeatable, peer-reviewed, and updated to capture new information and enhance expert judgment.

Recommendation 3. The framework used by USDA to evaluate imported plants for potential release as forage, crops, soil reclamation, and ornamental landscaping should be expanded to include rapid multitiered evaluation of the hazards that these species might pose. Controlled experimental field screening for potentially invasive species should be pursued for species whose features are associated with establishment and rapid spread without cultivation and whose immigration history is unknown. Similar efforts to acquire life-history and population level data in situations that approximate field settings would be beneficial in the case of nonindigenous insects and pathogens of concern, including species proposed for deliberate introduction.

DOCUMENTATION AND STANDARDIZATION

Recommendation 4. Information on invasions by plants and the pests of plants around the world should be assembled and updated regularly. Explicit information on new invasions in the United States—such as description of new locales, the partitioning of the species' genetic variation, and epidemiology of its spread—should be gathered and communicated more effectively to the scientific community; this information is essential in continually revising expert judgment. Careful recording of the circumstances of arrival, persistence, and invasion of nonindigenous species in the United States would substantially improve prediction and risk assessment.

Recommendation 5. A literature synthesis on the natural history of potential immigrant species, similar to the "Biology of Weeds" series published by the *Canadian Journal of Plant Science*, should be established, standardized, and made accessible via the Internet.

Recommendation 6. Information on the structure and composition of natural ecosystems in North America (and the disturbance regimes within them) should be reinterpreted by the scientific community to analyze these ecosystems' vulnerability to biotic invasion. Attention should be paid to identifying groups of native species that could be vulnerable or could facilitate the establishment of nonindigenous species.

Recommendation 7. A consensus on procedures to measure the impact of invasive species should be forged in the scientific and regulatory communities, and there should be more reporting of impacts of invasive species with standardized measures.

RESEARCH

Recommendation 8. Research on host specificity among pathogens and the correlation of some life-history traits (such as dispersal mode, reproductive system, and host range) with their documented ability to invade should be undertaken in relation to potential environments in new regions or areas. Question-oriented experimentation to elucidate relationships among species' traits and their new environments and hosts should be supported.

Recommendation 9. The release of nonindigenous organisms for biological control presents an opportunity to collect detailed demographic data on immigrant populations from the moment of their introduction. A substantial effort should be made to document the fate of these organisms, including the efficacy of the introduced organism on the target pest and on nontarget species, as a guide to the performance of unintended releases and as a mechanism to improve risk assessment in deliberate introductions of nonindigenous species.

Recommendation 10. Plants native to the United States that are growing in other countries, such as in botanical gardens and aboretums, should be monitored to determine the species to which they are susceptible and to evaluate the potential for these species to arrive in the United States. The severity of the damage to native U.S. plants by pathogens, arthropods, and other taxa, and the abiotic and biotic forces that contribute actively to the damage should be documented.

INFRASTRUCTURE AND EXPERTISE

Recommendation 11. A central repository of information relevant to immigrant species would accelerate efforts to strengthen the scientific basis of predicting invasion. Information collected by federal, state, and international agencies, academic researchers, and others should be brought together in a single information facility or service so that it can be evaluated collectively, to permit the construction of needed datasets and the design of appropriate experiments, and to document the circumstances surrounding invasions.

Recommendation 12. Focused scientific investigation is inadequate on nonindigenous species and prospective new environments from the overarching perspective of invasive potential. Multidisciplinary collaboration should be encouraged and supported among scientists with taxonomic expertise and those who specialize in population biology, community ecology, epidemiology, and simulation modeling. Multidisciplinary training of established and new investigators is needed to provide the expertise needed to make the study of invasion biology predictive.

In spite of a long history of interest in biological invasion, scientific inquiry in invasion is still nascent. Progress in understanding and predicting invasions will depend on how well the insights of investigators with diverse training can be coalesced and directed to decipher the myriad combinations of immigrant species, new ranges, and novel circumstances that can produce a biological invasion. The last 10 years has seen the emergence of a broad consensus that the prediction of biological invasion is a field of pressing national need. It will take some time, however, to generate the predictive principles on which policy-makers, regulators, the scientific community, and the public can have confidence.

Driving this sense of urgency is the growth in world trade of commodities and propagated material. The increasing volume of trade and the growing number of nations that are linked routinely to the United States through trade will undoubtedly result in the delivery of more nonindigenous species than ever before to U.S. ports of entry. With little or no biological information about these species that can be translated into risk assessment and prediction, APHIS will have difficulty evaluating and regulating them. The challenge of constructing a scientific basis for predicting the risk associated with nonindigenous species needs to be met by a significant national effort, including other agencies within the USDA, other branches of the federal government responsible for research and land management, agricultural and natural resource agencies of state governments, and the scientific community at large.

1

Introduction

Biological invasions are the uncontrolled spread and proliferation of species—including vertebrates, plants, arthropods, and plant pathogens—from their native geographic ranges to new ranges. Such invasions are recurrent worldwide phenomena, and their impact on the earth is an important component of global change (Mooney and Hobbs 2000). Federal and state agencies in the United States spend over a half-billion dollars per year to respond to the influx of nonindigenous (foreign) invasive species (GAO 2000).

Nonindigenous species that threaten plant performance, survival, and reproduction are referred to as plant pests; they include insects and other arthropods, microorganisms, and plants. Over the history of the United States, plant pests have left their mark on the national landscape, spreading into natural areas (as has the invasive tree *Melaleuca quinquenervia* in the Everglades), increasing the frequency and intensity of fire (as has *Bromus tectorum,* cheatgrass*,* in the Intermountain West rangelands), and even pushing native species to the brink of extinction (as has *Cryphonectria parasitica,* the chestnut blight fungus). Some nonindigenous insects and pathogens kill their host plants directly; others reduce plant vigor, thereby increasing vulnerability to other problems.

Few nonindigenous species that arrive become invasive. For example, most of the commercially important crop and horticultural plants used in North America are nonindigenous, and most of them require cultivation for their continued survival. The most economical and productive sites for many crops are often in locales far from the native ranges of their progenitors and from the pests that attack them in their native ranges (Freeman 1991). Even under the most favorable growing conditions, most crops fail to become invasive or even naturalized (that is, persistent but in low numbers) in new ranges.

The species that do arrive in the United States and become invasive, including the pests of nonindigenous crops, collectively affect the safety of our supply of food, fiber, timber, and water and the health of our domesticated animals and even humans. The cost of such invasions is probably incalculable. The aggregate figure for crop and timber losses and for the use of herbicides and pesticides to fight invasive species exceeds $100 billion per year, but this figure does not include the direct and indirect economic and ecological costs of invasions in ecosystems that are less intensively managed, such as forests, pastures, wetlands, and other wilderness areas (Pimentel et al. 2000).

As a result of the magnitude of the problem, scientists, crop producers, environmentalists, and public agencies are exploring ways to combat plant pests, beginning with preventing their entry into the United States. What might seem to be a straightforward endeavor is actually difficult. Regulating the arrival of nonindigenous species remains one of the most challenging tasks facing plant regulatory agencies today, because a major component of the global economy involves the transport of agricultural products, including the transfer of living organisms. Not only are agricultural products (such as grain, animal products, lumber, plant fibers, and cut flowers) being moved worldwide in unprecedented volume, but the use of imported germplasm that would give rise to these products in vast new markets is also increasingly widespread.

TROUBLE ON THE BORDER

The Animal and Plant Health Inspection Service (APHIS) of the United States Department of Agriculture (USDA) is responsible for preventing the introduction of plant and animal pests along human-mediated pathways. It carries out this mandate by prohibiting importation of known pests and by regulating the importation of commodities (such as fruits and vegetables), plants, and plant propagation materials that might harbor pests. APHIS agents at seaports, borders, and airports intercept restricted items such as food carried by tourists, and detect known pests that contaminate commodities, packing materials, and shipping containers. Although its monitoring activities in 1999 resulted in two million interceptions, which prevented the introduction of an estimated 53,000 plant pests (USDA 2000), the agency has the capacity to examine less than 2% of the cars, trucks, ships, and airplanes that bring products and people into the United States.

APHIS devotes much effort to evaluating the possibility that harmful pests will be contaminants in imported commodities and the significance of the economic or environmental damage that could result if these pests were introduced. Such evaluations are conducted on the basis of the probabilities of transportation and establishment and constitute the agency's assessment of the risk of introductions. Risk assessment is the basis of APHIS decisions to permit or restrict the importation of a commodity or to impose phytosanitary requirements, such as fumigation, that could exterminate hitchhiking pests. Risk assessments are most reliable when the identity and biological characteristics of a pest likely to be associated with a commodity are well documented and when the availability and vulnerability of potentially affected plants and their communities in the United States are known. Risk assessments are less reliable when it is not known which species might accompany a commodity or when known organisms are likely to be present but have an unknown capability to invade ecosystems and to harm plants in the United States. Even when much is known about the biological characteristics of a species in its native range, it can be difficult to predict the results of its entry into a new range. Intentional introductions of nonindigenous species for biological control of some specific pest, for example, have on occasion resulted in the introduced species' unexpectedly attacking species in addition to the targeted ones. Biological control species sometimes compete with and displace native species and have other unexpected effects (Louda et al. 1997, Lockwood et al. 2001). Consequently, release of these organisms requires careful prerelease screening and postrelease evaluation.

A parallel problem is posed by the importation of nonindigenous plant cuttings and seeds for horticulture and other uses. Some plants known to be invasive are on the federal noxious weed list, and these species are consequently prohibited from importation. If no information on their invasive potential is available, propagative materials are allowed to enter virtually without restriction.

The importation of propagative materials and commodities in the absence of definitive knowledge of their invasiveness weakens or even undermines the national system of plant protection. Even at the outset of any examination of these issues, it is clear that the predictability of invasiveness requires more scientific information and more effective use of existing information. The capability to use scientific principles and procedures to make such a prediction is urgently needed, not only to protect plant life, but also to fulfill U.S. commitments under international trade agreements.

The United States helped to establish the World Trade Organization (WTO) in 1995 to liberalize world trade opportunities. With more than 142 nation members, WTO maintains a code of trade rules and is a forum for discussing and adjudicating trade disputes. Disputes between nations can involve market access, export subsidies, domestic support schemes, and the sanitary and phytosanitary measures used by nations to dictate whether foreign goods may enter their borders on the basis of concerns for the health and safety of their citizens, plants, and animals. Before the creation of WTO, no international rules distinguished legitimate importation restrictions from trade barriers erected under the guise of protecting health or safety. Under WTO, the exclusion of any trade item must have a scientific basis (USDA/FAS 1999). The requirements apply as well to controls that the United States places on the movement of materials to protect this country from invasive plants and plant pests.

To clarify the basis of claims related to plant health, WTO, through the International Plant Protection Convention, sets international standards for phytosanitary measures in trade. Each country may establish its own standards, even if they are more conservative than the international ones, but they must be based on risk assessment and be justifiable scientifically.

The United States, as with other WTO members, is expected to benefit substantially from increased access to new markets for exports and from lower import prices for agricultural and forestry commodities. Trade liberalization in agriculture alone is expected by 2005 to raise world income by as much as $5 trillion and almost double the value of U.S. exports and imports (USDA/FAS 1999). However, trade liberalization increases correspondingly the likelihood that some of the hundreds of thousands of species of plant pests not yet found in the United States will someday arrive here.

APHIS is responsible for making regulatory decisions that simultaneously facilitate trade, comply with international laws, and reduce the risk of disseminating plant pests. That responsibility is daunting; APHIS needs whatever scientific tools are available to assist regulators in meeting potentially competing objectives.

SCOPE OF THIS STUDY AND STRUCTURE OF THE REPORT

APHIS asked the National Research Council's Board on Agriculture and Natural Resources (BANR) to review scientific knowledge about the characteristics of nonindigenous organisms, environments, and the process of invasion that could be used to refine inputs into its risk assessments, identify potential invaders, and guide the strategic allocation of its resources to safeguarding plant life in the United States.

BANR established the Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States, which comprises experts in invasive plants, plant pathology, entomology, horticulture, risk assessment, ecology, and population biology. The committee was charged to consider the available relevant historical and scientific data on plant, pathogen, and arthropod invaders and on the characteristics of plants that facilitate or impede invasions and to prepare a report that evaluates how scientific principles and procedures could be used to predict the invasive potential of nonindigenous plant pests. The committee met four times over a 12-month period, examined the scientific literature, and spoke to numerous experts on biotic invasions of agricultural and natural ecosystems.

In preparing its report, the committee undertook a four-stage analysis of the invasion process: the introduction of a nonindigenous species (immigration), its persistence at some threshold level (establishment), its proliferation and geographic spread (invasion), and finally the manifestation of its adverse effects on its new environment (impact). Chapter 2 deals with the factors that have historically influenced the accidental or intentional introduction of species into an area.

Although many nonindigenous species arrive in new ranges, few persist; Chapter 3 examines this important issue. Understanding the processes that allow persistence can have important implications for restricting the establishment of nonindigenous species before they become invasive. In Chapter 4, the committee examines the forces that facilitate or impede the proliferation and geographic spread of a plant pest, a stage at which a species can be said to be invasive. For most organisms, this stage is often the first process that can be observed directly; arrival and persistence usually occur without detection. Invasion is also the stage in which organisms can exhibit adverse impacts on the surrounding plant life and the ecosystem in general. The impacts of invasions have received the most attention by researchers and are examined in Chapter 5.

There is some overlap between components of this analysis, but the approach nonetheless serves as a common denominator among taxa, whether they are plants, arthropods, or plant pathogens. Even in the face of terminological, theoretical, and methodological differences among the scientific disciplines that study these organisms, the conceptual model allowed us to acknowledge the differences and facilitate their integration. In Chapter 6, the committee examines predictive methods and provides its own set of questions as a framework for using scientific information to predict the invasive potential of plants and plant pests. The chapter summarizes the ability to use scientific principles and processes to predict invasiveness and discusses implications of that capability for risk assessment.

Summaries of key scientific findings are listed at the ends of Chapters 2-6. In Chapter 7, the committee presents its overall conclusions and makes recommendations regarding research that is needed to improve the ability to predict invasiveness.

This report focuses on the threats of introduced plant pests to the plant resources of the United States. It does not explicitly include genetically modified organisms, although much of the same analysis would be relevant. Vertebrate pests are not included in the committee's charge, and aquatic plant resources, such as aquatic ecosystems and submerged aquatic vegetation, have largely been excluded. Otherwise, all forms of vascular plants–whether in agriculture, in forestry, or in natural areas in the United States–are topics of concern in this report.

2

Immigration: Predicting the Mode and Pathways of Introduction

> "A hundred years of faster and bigger transport has kept up and intensified this bombardment of every country by foreign species, brought accidentally or on purpose, by vessel and by air and overland from places that used to be isolated."
> (Elton 1958)

The distinguished British ecologist Charles Elton probably underestimated the scope of dispersal that had already caused the upheaval of the earth's biota by the 1950s. Human-mediated dispersal of organisms has occurred as long as organized, nomadic groups of humans have wandered across the earth (di Castri 1989). But in the last 500 years and expanding exponentially in the last 100 years, an increasingly large array of species have been transported to new geographic ranges that they were extremely unlikely to have reached without human assistance. Santayana's admonition that "those who cannot remember the past are condemned to repeat it" applies as well to predicting future nonindigenous threats to plants in the United States as it does to interactions among nations. We can safely predict that future introductions of nonindigenous invasive plants and plant pests will increase, driven by the seemingly inexorable growth in international travel and trade. Moreover, new modes and pathways facilitate the entry of known and potential pests into the United States. As a result, the potential for biotic invasions will increase unless appropriate science-based decisions in cooperation with our international trading partners are implemented to block the species' arrival.

In this chapter, we explore the sources, pathways, modes, and circumstances that have led to the immigration of species into the United States as a guide for predicting the species that could arrive and their means of arrival in the future. Historical accounts of introductions of nonindigenous species are invaluable in identifying the forces that facilitate the arrival of plants and plant pests, and they provide a basis for predicting the entry of other detrimental organisms. The implications of what we understand about pathways and modes depend on whether we are considering nonindigenous plants, arthropods, or plant pathogens. A chief distinction is that plants are usually introduced deliberately; arthropods and plant pathogens, except those introduced as agents of biological control or for confined research or public display (for example, in insectaria), are almost always introduced by accident. That difference has important implications for developing comprehensive predictors of the modes and pathways of entry.

NATURAL MODES AND PATHWAYS OF INTRODUCTION

The little we know about the arrival of plants and plant pests in North America and elsewhere by natural means is largely anecdotal (Ridley 1930). Clues to the likelihood and frequency of natural arrivals in the United States from distant places can be deduced from Smith's (1999) accounts of seeds that have drifted onto Australian beaches; such landfalls can generally be predicted from tides and currents. The numbers of nonindigenous species and their seeds that arrived in Australia were small, especially in comparison with the native species that drifted onto shore.

Natural dispersal of arthropods and plant pathogens over long distances does occur. Facilitated by migrating birds, mammals, and insects and by air and water currents, natural transport is best documented for plant pathogens. For example, *Pectobacterium (=Erwinia) carotovora*, which causes soft rot of fruits and vegetables, has been found in surface water, rain, clouds, and snow (Hirano and Upper 1990). Many fungal pathogens of plants produce enormous numbers of spores that are passively carried by wind over long distances (Nagarajan and Singh 1990). Yellow stripe rust of barley, caused by the fungus *Puccinia striiformis* f. sp. *hordei*, might have spread as windborne spores from South America to Texas via Mexico. Other examples of long-distance transport of rust fungi within Europe and between Africa and both Australia and South America have been documented. Spores of *Peronospora tabacina*, the cause of blue mold of tobacco, have been trapped over ocean and polar latitudes far from their source (Main et al., 1998). Whiteflies are vectors for several types of plant viruses; if carried by air currents, they might be a means of arrival of a virus (Polston and Anderson 1997, Polston et al. 1999). For example, Blair et al. (1995) speculate that bean golden mosaic virus might have been introduced via its whitefly vector from the Caribbean into the Homestead area of Florida by Hurricane Andrew. Similarly, the pink hibiscus mealybug (*Maconellicoccus hirsutus*), an Asian pest, was recently found in the Caribbean and is expected to be carried eventually to Florida by hurricanes (NAPIS 2000).

Natural pathways, however, appear to be a minor component of the global spread of nonindigenous species in contrast with human-mediated dispersal. The rates of organisms' arrival via natural dispersal to oceanic islands are instructive. The Hawaiian native flora might have resulted from a plant dispersal rate of only one species every 100,000 years (Fosberg 1948; Carlquist 1974), excluding introductions that failed to give rise to persistent species. Even at such a long interval, the 1094 native flowering plants in Hawaii could have originated from about 270-280 successful colonization events (Wagner et al. 1990). When Polynesians colonized Hawaii some 1500 years ago, they brought several dozen plant species with them (Nagata 1985), so the rate of introduction increased to one every 50 years. About 5000 plant species have been introduced to the islands since the beginning of European colonization, a rate of about 22 taxa per year (St. John 1973). At least 869 of these introduced species have become naturalized (persistent) in the last 200 years (Wagner et al. 1990).

In contrast, the natural rate of arthropod introductions resulting in establishment in Hawaii is estimated at one species every 175,000 years, assuming that colonization occurred over the entire history of the islands. The evolution of the total native Hawaiian insect fauna, estimated to exceed 10,000 species, required only about 400 colonization events during the 70 million years of existence of the island chain (Howarth and Mull 1992). The characteristics of the native insect fauna–including selective representation of insect groups, extensive radiation of some groups, adaptive shifts, and evolved flightlessness–reflect the youth of the islands, their extreme isolation, and the low rate of colonization by long-distance dispersal. Increasing contact with the outside world has broken down the biogeographic isolation that allowed for evolution of native island species and has led to its mixing with the world's biota. Today, at least 2500 insect species and 560 other land arthropod species in Hawaii are nonindigenous, and an average of 15-20 additional insect species become established each year (Beardsley 1979).

The rate of immigration of plants and arthropods via natural means appears so low as to cause little concern about the arrival of detrimental species. The arrivals of plant pathogens via natural forces have been documented and are more important than those of arthropods and plants. Even the best regulatory system will not exclude these immigrants, but the fact that some pathogen species can be dispersed in this way should be reflected in invasive-species management strategies.

HUMAN-MEDIATED ARRIVAL OF NONINDIGENOUS SPECIES

Predicting the character and course of biotic invasions is unusual in biology because a strong human component influences which species arrive in a new range. Knowledge of the human component does not necessarily reveal which species will become invasive, but it does provide important clues. Historically, the sources of nonindigenous pathogens, arthropods, and plants reflect trade and immigration patterns. For example, each wave of human immigrants to the

United States brought both accidental and deliberate introductions that have later become naturalized. Some have even become invasive (Mack 2001, Mack and Lonsdale 2001). Thus, not only do we see a strong early European origin of the nonindigenous biota of North America, but even regional differences among groups of Europeans have brought different species. Species immigrations have been more recently influenced by Caribbean, Asian, and other immigrant groups.

Accidental Introductions

Plants

Humans have long facilitated the accidental introduction of nonindigenous species of plants and their associated pests into new ranges in the United States. As early as 1672, Josselyn recorded the naturalization of several dozen nonindigenous plant species in New England (Mack and Lonsdale 2001). Although it is likely that many species were introduced before 1800, their accurate identification had to await the development of binomial nomenclature in the late 18th century. Consequently, our understanding of pre-1800 immigrants, including plants, is sketchy and tentative. The early publications of floras along the eastern seaboard all report convincing accounts of European species reputedly introduced as seed contaminants in hay carried as animal feed or in cargo (Pursh 1814). In some cases, the records are irrefutable because the original specimens have survived. Together, the late 18th and early 19th century published accounts (Pursh 1814) and herbarium and museum specimens provide substantial evidence of the arrival of nonindigenous species into Philadelphia, New York, Boston, and Charleston—all major pre-Revolutionary War ports of entry. Furthermore, the incidence of nonindigenous species along the Gulf Coast (for example, in Mobile and New Orleans) and later the West Coast (for example, in Los Angeles and San Francisco) tracks the growth of these seaports in commerce. Detailed surveys of the dry ballast (soil, rock, and building rubble) dumped along the shore around ports in the 18th and 19th centuries reveal that many foreign plants and insects, particularly beetles, arrived alive in the United States by this mode (Lindroth 1957; Baker 1986). Soilborne fungal or bacterial plant pathogens could also have been transported in ballast. Among the pre-1900 records are many cases of nonindigenous species that were reported once and have gone undetected (Rhoads and Klein 1993)—strong circumstantial evidence that the fate of most nonindigenous species is extirpation after arrival. As late as 1832, de Schweinitz's tally of the nonindigenous and troublesome plants in arable land was composed mainly of species that he ascribed to accidental introduction.

Later in the 19th century, the chronology of collection of herbarium specimens along the Pacific Northwest coast suggested that plant species entered the region at multiple sites, thus increasing the chance of their becoming established and invasive. Those species arrived at seaports and then moved along road and rail lines (Forcella and Harvey 1988). Freight and the packing material used in freight consisted of whatever material was at hand. Straw was a common packing material for fragile goods. And straw, in addition to often being grain stubble, can be a heterogeneous collection of pasture species, all of which can be represented by viable seeds in the straw. Dewey (1896) commented on the likelihood that species spread in the United States via straw; he noted the suspicious circumstances by which some newly arrived species in Denver first appeared near the back door of a crockery shop. Much less is known about the entry of nonindigenous species along the long common borders of the United States with Canada and Mexico. It is known, however, that some species (such as the annual grass *Bromus tectorum*) immigrated to the Pacific Northwest on both sides of the international border as accidental immigrants, as seeds in grain, or attached to livestock (Mack 1981). Current inspection standards limit the movement of weeds in grain, although many of those species (such as *Agropyron repens*, quackgrass; *Bromus* spp.; and *Chenopodium* spp.) are still accidentally moved through the United States (Westbrooks 1993).

Accidental entry accounts for only a small fraction of the newly naturalized plant species in the United States. With changes in production, shipping, and inspection practices, the rate of accidental introduction of nonindigenous plants has decreased. Seawater has replaced soil for ship ballast, eliminating a mode by which soil and soil-based nonindigenous species are transported. But as a result, the arrival of waterborne hitchhikers has been facilitated substantially (Carlton and Geller 1993). Changes in growing and production techniques—including the introduction of herbicides and the implementation of quality-control and inspection mechanisms associated principally with the 1939 Federal Seed Act and the 1957 Federal Plant Pest Act—have resulted in increased proficiency of APHIS inspectors in reducing the frequency of introduction of invasive plant seeds as contaminants of imported cereal crops, forage grasses, and produce and as hitchhikers on live animals (Westbrooks 1993). Entry of soil now requires a special permit and is thus inspected or treated, so soil itself is unlikely to be a source of entry of plants.

Insects

With the arrival of the Europeans, the long isolation of North America ended as geographic and ecological barriers to insect colonization were breached by commerce. From 1640 to 1980, the number of immigrant species of insects and mites resident in the 48 conterminous states rose steadily. Since passage of the Plant Quarantine Act in 1912, all plants and most plant products entering the United States have been subject to inspection, and action has been taken to prevent entry of arthropod pests. Before 1920, numbers of accidentally introduced insects had tended to increase exponentially; as the 1912 act took effect, the increase slowed to a linear rate (U.S. Congress 1993).

Despite increased detection efforts, interception of insects and other arthropods is difficult. Accidental introductions of nonindigenous insects and other arthropods are facilitated by their “hide and survive” attributes. Such traits as small body size, concealment (for example, under bark or in wood, buds, or roots), and cryptic coloration or structures that limit the visibility of an insect or pathogen facilitate “hiding” and reduce the likelihood that the organism will be detected in its place of origin or on its arrival in a new environment.

Historically, insects have accidentally entered the United States in three main modes: in ships’ ballast (Lindroth 1957), on introduced plants, and as a range extension from countries to the north or south. The proportions of immigrants representing different insect orders appear to change with changes in the relative importance of the mode of entry. For example, ballast traffic in the era of sailing ships was associated with frequent introductions of coleopterans, whereas later traffic in plant materials led to increased introductions of homopterans. Nursery stock remains a major source of introduction of insects (Sailer 1983).

Today, at least 2000 nonindigenous arthropod species are known to be established in the conterminous United States (U.S. Congress 1993), and 2500 nonindigenous arthropod species are established in Hawaii (Pimentel et al. 2000). Although nonindigenous insects make up only about 2% of the insect fauna in North America, they make up at least 40% of the species considered to be economically or ecologically important pests (Kim and McPherson 1993, Niemelä and Mattson 1996, Sailer 1983). An estimated 1000 nonindigenous insect or mite species are agricultural pests in the conterminous United States, and 98% of the insect pests of crops in Hawaii are nonindigenous (Pimentel et al. 2000). Sixteen insect orders, along with Acarina (mites), and Araneae (spiders) are represented among the nonindigenous arthropod species in the 48 conterminous states. Three orders (Hymenoptera, Coleoptera, and Homoptera) account for two-thirds of all nonindigenous arthropod species.

Europe has historically been a major source of nonindigenous arthropods. More than 50% of the nonindigenous insects now established in the United States originated in Europe (Sailer 1983), including 300 of the 400 species that feed on trees and shrubs (Mattson et al. 1994, Niemelä and Mattson 1996). An additional 200 European insect species have been established in the United States or Canada as a result of planned introductions for the biological control of insect or weed pests (Simberloff 1989). Less than 15% of the nonindigenous insects established in the United States or Canada are from Central America or South America, despite these regions’ proximity to the United States (Simberloff 1986, 1989). The disproportionate establishment of European insects is consistent with the biogeographic and climatic similarity between North America and Europe and the high level of commerce between the two continents over the last five centuries (Leibhold et al. 1995, Niemelä and Mattson 1996, Simberloff 1986).

There is a marked asymmetry in insect exchange between continents. For example, North America has gained about 300 species from Europe, but Europe has gained only about 40 species from North America. Vermeij (1991) observed that asymmetry characterizes most, if not all, biotic interchanges between biogeographic regions. Possible explanations for this phenomenon are discussed later in this report.

Pathogens

Most plant pathogens in the United States have entered inadvertently and unnoticed as contaminants of agricultural commodities, nursery stock, cut flowers, timber, seeds, and other plant parts and in the soil of potted plants, freight containers, packing material, and vehicles (U.S. Congress 1993, Pimentel et al. 2000). Imported collections of wild germplasm might have also been infected with viruses (Kahn 1991, Lenné and Wood 1991). Imported military cargo might have also been the source of hitchhiking pests. Soil on military and other used vehicles might have been the source of the corn cyst nematode (*Heterodera zeae*) (Sardenelli et al. 1981).

Despite an increase in trade and travel over the last half-century, fewer than five new nonindigenous plant pathogens were introduced in each decade from 1940 to 1970 (U.S. Congress 1993). The enactment of state and federal plant quarantine laws in 1912 are likely to have prevented an increase in introductions of pathogens commensurate with the volume of trade. During the 1970s, however, the number of newly introduced plant pathogens jumped to 18. Possible explanations include the globalization of agriculture, increasing commercial air traffic, and increased movements of seeds and plant material by the private sector spurred on by new intellectual property rights to plant varieties. The number of newly introduced pathogens dropped to seven during the 1980s. As of 1991, there were an estimated 239 plant pathogens in the United States whose origins are outside the United States (U.S. Congress, 1993). This number probably reflects the nonindigenous origin of most economic crops in the United States, the natural hosts for their respective nonindigenous plant pathogens. However, figures on detected pathogens undoubtedly represent organisms that have been recognized because they are causing notable diseases of economically important plant species. For most new disease outbreaks, researchers do not know, without population-genetics studies, whether an outbreak is due to an invasion or a previously unrecognized endemic pathogen that suddenly increases because of a change in cropping practices or environment. It is unknown whether plant pathogens already established in the United States might have spread beyond their native hosts to introduced crops. It might also be assumed that some nonindigenous pathogens have been introduced but remain undetected. There is a disincentive to survey for these, however, because of concerns of how such findings might affect some U.S. exports of plant-related commodities. Nevertheless, new technologies with increased sensitivity, such as polymerase chain reaction-based techniques, will become increasingly useful in separating indigenous from nonindigenous microorganisms and identifying their continent of origin (Martin et al. 2000).

Deliberate Introductions

Plants

Since the second half of the 19th century, most nonindigenous plants in the United States have been introduced deliberately. However, the origins of deliberate introductions of plants extend much further back into the history of agriculture in the United States. Regardless of the indigenous crop species available, the first colonists and their descendants had a strong preference for European crops, such as wheat, beets, onions, and brassicas. These species were repeatedly introduced; except for the weed species carried as contaminants in the seeds of these introduced crops, little harm occurred. One noteworthy exception, which is an example of how nonindigenous organisms can unexpectedly interact with indigenous ones, is the beet leafhopper (*Circulifer tenellus)*, which was introduced into the United States on the tops of sugar beets. It was later found to transmit an indigenous virus to sugar beets from native plants in semiarid regions of California and the Rocky Mountains, causing devastating losses to the sugar beet industry (Duffus 1971).

The introduction of nonindigenous species was not restricted to crops. English settlers along the eastern coast of North America in the 17th century soon became dissatisfied with the quality of native forage. One 17th century settler in New England complained that the native forage "is so devoid of nutritive vertue, that our beasts grow lousy with feeding on it, and are much out of heart and lung" (Cronon 1983). Securing nutritious forage was a serious concern for settlers who had neither the time nor the inclination to experiment with native species as forage. By 1635, those planning to settle in Maryland were cautioned to bring a "good store of Claver grasse seede, to make good meadows" (Edwards 1948). The native species clearly had been dismissed as unsuitable.

Much American folklore to the contrary, the Intermountain West of the United States is only marginally suitable for livestock; the principal native grasses, all bunchgrasses, are intrinsically intolerant of persistent grazing (Mack and Thompson 1982). As a result, the abundance of these grasses was radically reduced by 1900, less than 50 years after the wholesale introduction of cattle and sheep. By 1900, many had concluded that "the native grass is gone, and experiment has not yet fully demonstrated the adaptability of any other grass to this soil and climate" (Anon. 1901 as cited in Mack and Thompson 1982). The call went out rapidly for species from Eurasia. Little or no effort was spent in exploring the native species; nonindigenous grasses—such as *Agropyrum cristatum* (crested wheatgrass), *Bromus inermis* (awnless brome), and even the highly invasive *B. tectorum*—were soon being evaluated as substitutes (Mack 1981). Only a few of these nonindigenous species (such as *Agropyron cristatum* and *A. desertorum*) have been judged even marginally suitable as forage, and some could produce plant invasions, such as *Kochia prostrata* (kochia) and *A. repens* hybrids (Mack and Thompson 1982, Mack 1999).

Those introductions were organized into commercial ventures surprisingly early. Seed merchants, whose trade dealt primarily with the importation of nonindigenous species, were advertising their stock in broadsheets by 1800 (Mack, 1991), and this cottage industry grew enormously in scope and national distribution in the 19th century. Most important here is that the array of species greatly expanded from small lists of crop plants and a limited number of medicinals to a wide array of plants for seasonings and ornamentation. These private endeavors with their international contacts were augmented and even supplied by government agencies. As early as 1827, President John Quincy Adams issued a formal policy of encouraging and facilitating the entry of any "plants of whatever nature whether useful as food for man or the domestic animals, or for purposes connected with manufactures or any of the useful arts" (Mack and Lonsdale 2001). An early mission of the U.S. Department of Agriculture was the distribution of these plants and animals to American farmers.

We will probably never know accurately the size of the pre-1800 adventive and naturalized flora in the United States. On the basis of tallies from early floras, it was at least 100 species. By 1832, it had grown to about 150 species (de Schweinitz 1832), but it tallied over 400 species by 1859 (Darlington 1859). By 1900, the number had increased to well over 600 (Gray 1889); and it has risen steadily ever since. Today, various estimates place the naturalized flora of the United States as 2000-3000 species (Kartesz 1994).

Insects and Pathogens

Insects have been deliberately introduced into the United States for biological pest control, for pollination, and as pets. There are many nonindigenous arthropod species in the pet trade; most are produced domestically, but there is still a considerable volume of importation for pets, "feeder" organisms (live reptile food), and fish bait. Pet-trade organisms include millipedes, tarantulas, other spiders, scorpions, centipedes, whip scorpions, preying mantids, and other predatory insects that could affect plant resources via intermediate organisms. Walkingsticks, crickets, and cockroaches are of perhaps the greatest concern for regulators because they can cause direct harm to plants. Some have already reached pest status, such as the Indian walkingstick (*Carausuis morosus)*, which required control on at least three occasions—once in southern Maryland or Virginia in the 1990s and twice in California in the 1980s. *Acheata domestica*, the common European house cricket, is sold nationwide as a feeder cricket and is proposed for deregulation. It is established across most of the United States.

The honeybee (*Apis mellifera)* was intentionally introduced from Europe for honey and crop pollination and is now very common and interacts with other species. The spread of a new form of the honey bee, the Africanized bee, from Brazil across South America, through Central America, and into the United States is a spectacular invasion with economic and other consequences for human life (Winston 1992).

Insects and, to a lesser extent, pathogens also have been deliberately introduced into the United States since around 1950 for biological weed control. The United States (including Hawaii), is the leading importer of nonindigenous organisms for biological weed control—130 agents released by 1990, followed by Australia (123 biological agents), South Africa (61), Canada (53), and New Zealand (24) (McFadyen 1998). As of the end of 1996, there were at least 1150 planned releases of 365 species of invertebrates and fungi on 133 weed species in 75 countries (Julien and Griffiths 1998). About 61% of released organisms become established, and about 32% of established organisms contribute to control (Lawton 1990). Worldwide trends show the release of species for biological control increasing faster than the introduction of designated target organism species (Julien and Griffiths 1998), and biological control efforts in the western United States follow the same trend (McEvoy and Coombs 2000). Some have argued that the increasing number of biological control experiments may be making pest control less effective and riskier (McEvoy and Coombs 1999). Although most nonindigenous insects and pathogens that are plant pests have been accidentally introduced, biological control organisms have themselves become pests on occasion.

PREDICTING ARRIVALS OF NONINDIGENOUS PLANT PESTS

The issues related to predicting the arrival of plants differ from those related to the arrival of pathogens and insects. The introduction of most nonindigenous plants is intentional; the introduction of insects and pathogens is mostly unintentional. For unintentionally introduced organisms, it would be useful to identify the mechanisms that facilitate their entry into the United States, the origin of the commodities with which specific arthropods and pathogens are associated, and any traits that may have facilitated their introduction.

With regard to plants, 96 plant species are on the Federal Noxious Weed List and are prohibited entry into the United States, although the effectiveness of this prohibition has not been quantified. Cuttings and seeds of plants that are not on the Federal Noxious Weed List may be imported, provided that they are not shown to harbor plant pathogens or arthropods. Not being included on a federal list does not mean, however, that an introduced plant will not eventually become a pest. The history of the importation of plant species into the United States and elsewhere is littered with the disastrous results of imprudent choices for introduction (Lonsdale 1994, Mack and Erneberg in press). Therefore, it would be useful to know more about the plants being introduced into the United States—the origin of the plants, their ecology in their native environments, and any biological characteristics that may contribute to their invasive potential.

Trends That Influence the Unintentional Arrival of Nonindigenous Plant Pests

In the absence of comprehensive information on the location, identity and characteristics of all the plant pests in the world, predictions that plant pests will arrive are based largely on history and on the identification of trends that increase the risk of introductions in the future. For example, we know that international trade in agriculture is a major source of nonindigenous pathogens and arthropods. Of the food consumed in the United States, 10% is imported, and horticultural products, including fruits and vegetables, top the list (USDA/ERS 2001). In addition, human travelers contribute to the inflow of pathogens by arriving with contaminated plants and foods. In one week in May 1990, an inspection of 16,997 passengers arriving on international flights at the Los Angeles International Airport led to the interception of 1357 lots of fruits and vegetables and 325 lots of animal products, for a total of 2635 kg of contraband plant material (U.S. Congress 1993). As with world trade, tourism is increasingly important as a mode of introduction of nonindigenous organisms. During the 1980s and 1990s, tourism became an emerging sector of the economy, contributing $26 billion in 1986; it has since risen to more than $110 billion per year. Over 46.5 million international visitors entered the United States in 1996, and the projected annual growth rate is 3-4% (Doggett 1997).

The spread of plant pests has been facilitated as intercontinental air commerce has flourished. No longer must an immigrant species be conveyed from an interior area to a seaport for embarkation, survive the sea voyage, be unloaded, and then be conveyed to an interior locale. The speed of air traffic has meant that cargo that accidentally or deliberately contains eggs, seeds, spores, or any other living stage of an organism can be transported from almost any point on the globe to the United States within 24-36 hours— well within the survival time of a great array of species, compared with the weeks or months at sea that can be fatal for many species. Such inland cities as Denver, St. Louis, and Dallas are now major points of disembarkation for all manner of air cargo, and a multitude of much smaller cities and even rural areas also receive international flights. This traffic includes agricultural products and increases the possibility that invasive organisms will reach vulnerable locations.

The use of containers for seaborne cargo has seen a steady increase since its introduction in the middle 1960s. In 1992, 9% (by weight) of all U.S. agricultural exports moved in containers; in 1998, the fraction increased to 13% (USDA/AMS 2001). The universal adoption of containers in shipping might also affect detection of known, invasive species, especially if containers are not opened until they have been carried far inland. Consequently, infestations are no longer confined to port areas but can arise at any place in the country or simultaneously in more than one place. All major metropolitan areas (and many smaller ones) are now points of first-time entry of species that have the potential to become invasive.

Some organisms arrive in the United States through illegal transport (Yee and Gagne 1992, Schmitz and Westbrooks 1997). To an unknown degree, the transport of ornamental, crop, and illicit drug-producing plant materials creates an additional array of points of entry for plants, arthropods, and pathogens that are extremely difficult to monitor. A much larger concern arises with the smuggling of prohibited agricultural fruits and vegetables, such as Mexican avocados, that may harbor pathogens or other pests (Nyrop 1995, Firko 1995b); with the North American Free Trade Agreement (NAFTA), the potential for this traffic has probably increased.

Trends That Influence the Intentional Importation of Invasive Plants

As discussed earlier, most plants are introduced intentionally (legally or illegally), and the invasiveness of many plants is not established well enough to warrant their inclusion on the Federal Noxious Weed list. Most nonindigenous plants that became invasive did not express their invasive ability immediately after arrival.

In the meantime, the search continues for new commercial crops to broaden our food base, as does the questionable enthusiasm for introducing new nonindigenous forage species (Lonsdale 1994, Mack 2001). But those uses of nonindigenous plants pale in comparison with the public's enthusiasm for importing plants for horticultural landscaping and gardening. As outlined below, such desire for ornamental plants creates the chief threat of entry, establishment, and spread of detrimental nonindigenous plant species.

In 1997, the floriculture and horticulture industries had cash receipts of $11.2 billion (USDA/ERS 1999). Plant enthusiasts participate in informal, international seed exchanges, and a few retail and wholesale nurseries and arboretums have active plant exploration programs. Their expeditions include collecting plants in the wild and purchasing local favorites from foreign nurseries. Many nurseries still sell plants that are potentially invasive. Most retail nurseries sell only locally, so an invasive plant species might pose a problem to only a small area; this facilitates its control if it is recognized early as a threat. Some retail nurseries, however, operate mostly or completely by mail order, and they ship species virtually anywhere. As in the early commercial seed trade in North America, wholesale shipping and retail postal shipment increase substantially the probability that an invasive species will be introduced into many more habitats, thereby increasing the likelihood that it will be introduced in or near a highly suitable or otherwise vulnerable environment. At least 82% of the 235 woody species that are invasive in the United States were introduced for horticulture (Reichard 1997).

Future plant importation can also be expected to stem from a perceived need for new species for erosion control, especially in land restoration and reclamation (U.S. Soil Conservation Service 1988). That perception will spark importation of a comparatively small number of species (perhaps several hundred), but the number belies their potential importance as a source of future invasions. Unlike ornamental or crop species, these species will be selected for their ability to persist with little or no cultivation. In the least damaging outcome, they would reside on a site, but their persistence would depend on recurring planting or reseeding. Much less desirable from a conservation standpoint, they would become naturalized; at worst, they would become invasive. Predicting problem species in this group is somewhat easier than predicting invasive species arising from horticultural introductions. Many of the traits sought by restoration workers in new imports also enhance naturalization and invasiveness: rapid growth, lack of specificity to soil type, low soil-nutrient requirements, deep roots, frost tolerance, vigorous vegetative propagation in addition to sexual reproduction, fibrous root system, and, perhaps worst, a fruit that shatters on maturity (Mack 1989 and references therein). Nonindigenous species that can colonize a bare surface rapidly and remain persistent without maintenance might be deemed advantageous in land reclamation, but they have the potential to become invasive.

The recent interest in herbal medicines can lead to the introduction of nonindigenous and potentially invasive plants. Unlike species introduced for land restoration, these species might require substantial and continuous cultivation and present no threat of invasion. But among plant species cultivated as both herbal remedies and seasonings are some that have become naturalized and a few that have become invasive. *Hypericum perforatum* (St. John’s wort) is emblematic of the risk posed by herbal species. It was first introduced into the United States in the late 18th century for its reputed medicinal properties (Haughton 1978). By the middle of the 20th century, it was a major invader in rangelands in the western United States, but its spread was reversed through biological control in the 1950s (Huffaker and Kennett 1959). (It was not, however, eradicated.) Ominously, new foci in its U.S. range are being established in response to interest in its reputed powers.

Informal seed exchanges, many of which are managed by amateur gardeners, constitute another market for plants. One advertisement on the Internet offers the following species for sale as medicinal plants: *Atropa belladonna* (belladonna), *Berberis vulgaris* (European barberry), *Cynoglossum* sp. officinale (hound’s tongue), *Dipsacus sylvestris* (teasel), *Echium vulgare* (viper’s bugloss), *Hypericum perforatum* (St. John’s wort), *Isatis tinctoria* (dyer’s woad), and *Silybum marianum* (variegated thistle). Each is deemed a pernicious weed in at least part of the United States. Other troublesome species available from the same purveyor were *Ailanthus altissima* (tree of heaven), *Casuarina equisetifolia* (common ironwood), *Passiflora mollissima* (banana poka), *Psidium* (probably *P. cattleianum,* strawberry guava), *Ricinus communis* (castor bean), and "Chinese tallow tree, *Sapium*" (probably *S. sebiferum*). These species include not only plants of ornamental value, but also those valued as medicines and seasonings.

Recognition of the importance of identifying the sources and characteristics of potential immigrant plant species is heightened by the recognition that only a small fraction of the earth's flora has ever been introduced into the United States. For example, the worldwide vascular-plant flora consists of some 250,000 species. Admittedly, a large fraction of those species are native to lowland tropical environments that have no counterpart in the United States—even in Florida, Hawaii, and Puerto Rico—and consequently pose little or no threat. But another fraction of the world's flora, at least as large as all foreign species in the United States today, have yet to be introduced, and the potential for their naturalization cannot be ruled out without further evaluation.

Increased opportunity for collectors to reach heretofore inaccessible parts of arid southern Africa and Arabia present the likelihood that some native species from these regions will become naturalized in the arid United States. The zeal of some private parties for collecting succulents and other drought-tolerant species is extraordinary (Mack 2001). Some amateur collectors now have hundreds of species in their gardens, products of their own collecting trips for aloes and other succulents in Yemen, Madagascar, and southern Africa (Levick and Lyons 2000). Plants can escape from arid gardens. For example, the attractive perennial grass *Pennisetum setaceum* (fountain grass), a native of north Africa, is now widely sold in the United States (Isaacson 1996) and has become naturalized in Arizona and southern California (Hickman 1993). As recently as 10 years ago, it continued to escape from commercial nurseries in southern California into adjacent desert communities (R. N. Mack, personal observation).

Any estimate of the number of invasive plants that will arrive in the future is admittedly, and of necessity, rough; it is based entirely on past trends. Whatever the number of plant invasions now in the United States, which is itself disputed, they arose from all the plant species that have ever been introduced. There is no firm figure for these introductions, and we probably cannot derive a direct estimate. However, some 40,000 taxa are commercially available in the United States today (Issacson 1996), including about 2000-3000 naturalized species and more than 300 truly invasive species; so we can predict that entry of *another* 40,000 species might produce several hundred new plant invasions.

The Port Information Network (PIN) Database

Although judgments about what is likely to occur can be based on historical or projected trends, the national database of plant pests intercepted at U.S. ports of entry is perhaps the best source of information on the number and identity of nonindigenous plant pests arriving in the United States. The Port Information

Network (PIN) database has been maintained by APHIS since 1985. Information in as many as 37 categories is collected when an APHIS inspector finds a pest with potential quarantine significance.

Roughly 53,000 such interceptions are made each year in arriving cargo or baggage. Arthropods, primarily insects, make up 60 to 65% of the records, plant pathogens 25%, plants that are deemed weeds 5%, and snails and other taxa comprise the remainder.

There are recognized limitations in the quality of PIN data. Sampling protocols are not implemented on a consistent and statistically designed basis, and this makes comparisons of interception data between years or locations less reliable. The data underestimate the number of insects or other pests arriving because only one record (for each species) is submitted per interception event, regardless of the number of organisms of a species that are detected in the intercepted shipment. In addition, only organisms determined by APHIS to be "reportable" or "actionable" are recorded. Species that are already widespread or insects that do not threaten plants (such as parasitoids and fungivores) are not included in the PIN database. Limited resources also prevent APHIS personnel from recording negative results; for example, inspections that produce no reportable pests are not recorded. Determining the origin of pests intercepted on cargo is generally straightforward, but identifying the origin of pests intercepted in baggage is often problematic. For example, if fruit flies are intercepted on a mango confiscated from a tourist arriving from France, the only known origin of the fruit flies is France, but the source of the mango and its associated pests was presumably a tropical country. Survey and detection resources and systematic expertise can vary among ports. APHIS entomologists are usually present at ports of entry, but smaller ports might lack plant pathologists or botanists on site. Moreover, techniques to assay for pathogens are unavailable or underused. Organisms of concern (or digital photos) can, of course, be forwarded to specialists for identification, but the process might require that travelers or cargo be detained until the identification is made.

Despite their limitations, the PIN data can be used to develop profiles of pest interceptions at a given point of entry, identify training needs for inspectors, and help regulatory officials to anticipate the arrival of pests that are more likely to be associated with specific imported commodities. More generally, PIN data can be used to assess patterns in the arrival of nonindigenous insects and reveal how the patterns may change in time or vary among ports.

For example, Haack and Cavey (1997) used PIN data to assess nonindigenous insects arriving in the United States on wood packing and crating material. In 1985-1996, 5885 insects originating in 87 countries were intercepted in wood material at U.S. ports. Although 10 orders and at least 54 insect families were intercepted during the 12-year period, almost 95% of the insects were beetles (order Coleoptera). Nearly all the insects were bark beetles or wood borers. Those insects present a clear concern in detection and eradication because much of their life cycle takes place hidden under bark or in wood and because many of these species can be important pests of forest or shade trees.

In tallying the origin of all insects associated with wood, Haack and Cavey (1997) found that about 75% of the interceptions stemmed from 10 countries, including six European countries (Italy, Germany, Spain, Belgium, France, United Kingdom)—a pattern that would be expected, given the historical and current volume of trade between these countries and the United States. One notable finding was the sharp increase in the percentage of interceptions originating in China in 1992-1996, a period that coincided with the dramatic jump in trade between the United States and China. The value of agricultural imports to the United States increased by 58% in 4 years, from $279 million in 1992 to $442 million in 1996 (USDA/ERS/FATUS 2001). Asian countries could be an increasingly important source of nonindigenous insects, especially if green wood continues to be used as a packing material for imported goods (Haack and Cavey 1997). Recently implemented regulations require that wooden crates, dunnage, and related wood packing material originating in China be fumigated, kiln-dried, or treated with preservatives; and standards were set for the maximal amount of permissible bark on wood packing material (USDA/APHIS 1998). Continued analysis of PIN data will help to determine the effectiveness of the new regulations.

As noted earlier, nursery stock is consistently a source of introduction of nonindigenous insects. For example, Sailer (1983) reported that 20% of nonindigenous insects established in the United States were initially introduced on nonindigenous plants. More recently, McCullough and Cavey (unpublished data) examined a subset of PIN data collected in 1990-1999 and identified the insects and other plant-feeding arthropods intercepted at U.S. ports on imported plant material intended for propagation; they also determined the origin of these insects. The propagative material included whole plants, bulbs, and roots, stems, or leaves used for propagation.

In the ten-year period, 14,878 arthropods representing at least 15 orders and 85 countries of origin were intercepted on the plant material. Those organisms made up more than 20% of all interceptions and 35-40% of all arthropod interceptions recorded in the PIN database. Homoptera accounted for 30.2% of all intercepted arthropods, followed by Acarina (16.3%) and Lepidoptera (9.2%). Coleoptera and Orthoptera each accounted for 7.2%, and Thysanoptera accounted for 3.2%. About 20% of intercepted arthropods were not identified as to order, usually because specimens were badly damaged or desiccated or were present only as eggs without distinct taxonomic characteristics.

Haack and Cavey (1997) found that most arthropods in wood were introduced from Europe. Analysis by McCullough and Cavey (unpublished) showed that most arthropods intercepted on plant material intended for propagation arrived from Mexico or Central American countries (See Table 2-1). Intercepts from China, Singapore, and Japan were also common; insects from these countries

TABLE 2-1 Arthropod Interception on Plant Material Intended for Propagation: 12 Countries with Highest Number of Interceptions

Origin	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Total
Costa Rica	386	285	144	318	336	378	574	741	838	723	4723
Guatemala	110	143	101	104	180	151	140	186	223	118	1456
Mexico	148	124	70	123	93	120	101	119	154	141	1193
Netherlands	101	99	67	108	97	94	108	89	82	57	902
Honduras	110	43	21	85	162	77	104	106	117	61	886
Thailand	83	121	94	80	70	73	67	62	63	57	770
China	41	40	39	41	64	78	77	77	62	69	588
Singapore	49	56	37	41	42	46	51	65	50	61	498
Japan	60	40	35	18	34	35	17	33	30	37	339
Belize	33	18	18	47	30	20	22	13	26	5	232
South Africa	6	23	10	16	28	36	14	38	28	18	217
Dominican Republic	53	15	6	24	21	24	15	18	18	6	200
Total	1180	1007	642	1005	1157	1132	1290	1547	1691	1353	12004

SOURCE: PIN data 1990-99.

may pose a greater threat if the importation or propagation of Asian plants continues to increase as projected. Of European countries, only the Netherlands, the world's top exporter of plant material in the horticultural trade, was represented in the top 12 originating countries.

Interceptions were made at 20 seaports and airports, but more than 70% of all interceptions occurred at three ports - Miami, JFK International Airport (New York), and Los Angeles. At the Port of Miami, Costa Rica and four other Central American countries were the source of over 80% of the interceptions. Interceptions at JFK International Airport were dominated by organisms from Europe and Asia, including the Netherlands (30.1%), China (10.7%), and the United Kingdom (5.3%). At Los Angeles, the most common countries of origin of infested plant material were Costa Rica (15.2%), China (13.5%), Thailand (13.1%), and Guatemala (9.6%). Each of those points of entry serves a different sector of the incoming international cargo: New York, European goods; Miami, Central American goods; and Los Angeles, Asian goods.

The ecological significance of those proportions stems from the different likelihood of establishment of nonindigenous species at or near their point of disembarkation. Miami is an ideal U.S. entry point for the survival of organisms from Central America. In contrast, for much of the year, the physical environment of New York poses a hazardous environment for immigrants from tropical climates but could be suitable for diapausing species arriving from temperate climates in Europe or Asia.

Although the results summarized briefly here represent a modest effort to categorize a subset of the PIN data, more extensive analyses and access to other regulatory databases would be highly useful for predicting the arrival of nonindigenous species. For example, the likelihood that a nonindigenous insect species will become established depends in part on the frequency of its introductions and the number of immigrants arriving in each introduction (Williamson and Fitter 1996, Levine and D'Antonio 1999). If an arthropod species is frequently intercepted, especially in large numbers, the risk that its immigrants will eventually escape detection and encounter an environment suitable for their persistence may be high. That hypothesis should be testable if accurate interception records are maintained. There are also opportunities to identify specific host plants or traits of host plants that are frequently associated with hitchhiking arthropods. Persistent patterns could identify commodities that require enhanced regulation or inspection before the commodities enter or are distributed in the United States.

Strengthening the quality of the PIN database and increasing the availability of the data for analysis of patterns or traits associated with inadvertent introductions of plant pests is a potentially important first step in developing better hypotheses about the characteristics of potential invaders and the pathways by which they arrive at the borders of the United States. Given the complexity, size, and inconsistencies of the PIN database, such analyses will require participation of APHIS officials who can provide background information to prevent investigators from reaching incorrect conclusions. Ideally, analysis of PIN data would involve collaboration of APHIS officials, biometricians, and scientists with expertise in specific taxonomic groups or aspects of invasion ecology.

China: A Likely Source of Many New Species in the United States

In predicting future invasive plants, arthropods, and plant pathogens, China should be considered a prime donor region. Identifying China as a major source of future immigrants with the potential to become invasive has ecological, historic, and economic explanations. In its range of physical environments, China contains an extraordinary parallel to those found in the United States. Among nations, it alone has counterparts of the range of physical environments (from tropical to arctic) found in the United States (Hou 1983). Its flora, which contains about 30,000 vascular plant species (Brach 1998, Axelrod et al. 1998), includes many taxa that play ecological roles comparable with those played by native species in natural communities in the United States (Qian and Ricklefs 1999). China contains temperate deciduous forests dominated by oaks, ashes, and birches that are congeners of species occurring in similar roles in U.S. forests. China's temperate coniferous forests illustrate the physiognomic and floristic similarity to U.S. coniferous forests: forests dominated by *Abies, Picea,* and *Pinus* (Wang 1961). These parallels between species in the United States and China suggest that Chinese species could assume similar roles in U.S. natural communities if they were introduced. Of course, their introduction does not necessarily ensure their naturalization or invasiveness.

The acquisition of nonindigenous plants, especially species heretofore unknown in cultivation, remains a strong motivation of plant collectors. In this regard, Europe and North America represent probably only modest potential for providing species new in horticulture, because their floras have been searched for horticultural species for centuries. The floras of South America and Australia have been less exploited for this purpose, but large fractions of them consist of lowland tropical species that have limited commercial value in the United States for landscaping. Future naturalizations will probably arise instead from regions insufficiently explored for horticultural species. China is a prime source of horticultural species.

For centuries, Europeans held a fascination with the Far East, including its plants. Although trade with the Far East, especially in perishable plants, was infrequent and difficult (Cox 1945), enough was known of its floras by 1800 to suggest that many of its species would tolerate the climates of Western Europe (Spongberg 1990). Collectors, employed either by governments or by wealthy patrons, criss-crossed the Far East throughout much of the 19th and early 20th centuries (Musgrave et al. 1999). They were largely responsible for introducing European and North American collectors to the floral diversity of eastern Asia

(Cox 1945, Spongberg 1990). Among the species they introduced into the U.S. horticultural trade are some notorious plant invaders. George Rogers Hall collected *Lonicera japonica* (Japanese honeysuckle) (Spongberg 1990). Thomas Hogg reputedly introduced *Pueraria lobata* (kudzu) (Spongberg 1990), the scourge of disturbed land in the southeastern United States (Westbrooks 1998). Even if Hogg was the first purveyor of kudzu, he probably was not the last; it was available directly from Japan in the 1890s and also appears among the accession records of the U.S. Plant Introduction Service (Mack 1991).

The attractions that drew 19th century plant collectors to China remain: a diverse flora in a variety of environments that are similar to large swaths of North America and western Europe (Qian and Ricklefs 1999). In a sense, the work of the early collectors was interrupted. As China became increasingly unstable politically early in the 20th century, western plant collectors suspended their operations (Spongberg 1990, Mack 2001). As a result, there was little or no exportation of horticultural species or plant collecting by westerners until recently (Valder 1999). Collections of crop species, such as soybean, however, have been extensive in recent years.

Resumption of large-scale sustained trade with the West means that Chinese horticultural material can and will once again be exported in quantity. Seventy-five years of little or no opportunity for plant exportation from mainland China by western horticulturists has created much pent-up enthusiasm for new horticultural species from the temperate world's last great unexplored natural repository. The recently published *The Garden Plants of China* begins, "Nowadays it is possible once more to visit most parts of China, to repeat and extend the journeys of the famous plant explorers of the past, and to collect many beautiful plants not previously brought into cultivation or, in many cases, even known" (Valder 1999). Such unbridled enthusiasm could substantially increase the number of species arriving into the United States without appropriate attention to the potential for these immigrant species to become invasive.

Economic signs are clear that trade with China is burgeoning. In the last decade, the value of agricultural imports from China has more than doubled—to $758 million in 1999 (USDA/ERS/FATUS 2001). This trade will probably increase. In November 2001, China hosted its first international exhibition in Beijing to promote the export of Chinese seed and germplasm. The increase in trade creates opportunities for the introduction not only of plants, but also of pathogens, such as those associated with crop species, and of insects, such as the Asian long-horned beetle, which arrived in wood packing material.

KEY FINDINGS

- Almost all nonindigenous plants, arthropods, and pathogens in the United States were transported in the United States by humans. Natural introductions (via wind, birds, and so on) of pathogens have occurred occasionally but are rare for other taxa. The role of humans as the chief dispersers of nonindigenous species into the United States will continue.

- The rate of introduction of invasive plants, arthropods, and pathogens will increase in the future because of continuing growth in international travel and trade.
- Most arthropods and pathogens arrive into the United States accidentally. Attributes that enable these organisms to escape detection and to survive in transit facilitate their arrival.
- Arrival rates of nonindigenous arthropods and pathogens are probably related to the abundance of the species in their native habitats, the geographic areas of their native habitats, their association with plant materials that are likely to be imported into the United States, and the volume of trade between donor countries and the United States
- Most plants that arrive in the United States are intentionally introduced. New pathways that facilitate the arrival of invasive plant pests include importation of nonindigenous species for herbal medicines, Internet-assisted exchanges of seeds or plants, and commerce in species new to horticulture. Such informal exchanges are largely unregulated and unmonitored.
- China is a potentially major donor of future invasive plants, arthropods, and pathogens. This new situation reflects the recent radical increase in trade after a long hiatus and the similarity of physical environments in China and the United States. Such trade is the chief source of introduced plants that could become invasive—plants for ornamental horticulture. For example, there is strong interest in the importation of new horticultural taxa from China. This interest could lead to the arrival of new invasive plant species and provide increased opportunities for hitchhiking arthropods and pathogens to arrive in the United States. Many plant-feeding insects and pathogens from China would have a high probability of encountering susceptible families or genera of hosts in the United States.
- The Port Interception Network database maintained by APHIS since 1985 is an important source of information about the arrival of nonindigenous species. Although the detail and comprehensiveness of its data are limited, they do identify the species arriving at specific U.S. ports and borders, and the origin of the commodities associated with them. Collaborative efforts between APHIS officials and scientists to expand the information content of the PIN database and to use the data to assess patterns in arrivals and traits associated with frequently introduced species would prove informative.
- Europe was historically the primary source of invasive nonindigenous plant, arthropod, and pathogen species in the United States, and nonindigenous species continue to be intercepted at high rates on some commodities from Europe.

- The widespread use of containers in shipping, the growth of international airline commerce, and the illegal transportation of plant materials into the United States increase the likelihood that nonindigenous plant pests will survive transit to the United States and increase the difficulty of intercepting plant pests.

3

Establishment

Establishment refers to the apparent persistence of a population and is equivalent to the term *naturalization* as used for the descendants of plant immigrants (Mack 1997). To become established or persistent, immigrant plants, arthropods, or pathogens (or their descendants) need not be widespread or growing rapidly, but they must withstand challenges to their survival. The challenges include the random events that often prove detrimental to the survival of small populations, including a potentially hostile climate; inadequacies in nutrients, hosts, or mates; and competitors and predators. The vast majority of immigrant populations do not become established. For example, although thousands of nonindigenous phytophagous insects arrive in the United States every year, establishment is a rare occurrence (Carey 1996, Lewis and Kareiva 1993). Only an estimated 10% of all nonindigenous insect species that are introduced into a new range become established. Even when insects are carefully selected for intentional introduction as biological control agents, only about 33% become established (Williamson and Fitter 1996).

How does a species become established in a new geographic range? Studies dealing with that question have focused on the environmental forces that impede establishment while identifying particular circumstances of an introduction, such as the size of the founder population or the species' traits, that might facilitate its ability to overcome that impediment. For example, it has been recognized for more than 150 years that immigrants into a new range gain a substantial potential advantage by leaving behind their native competitors, natural enemies, or other biotic constraints on growth, development, survival, and reproduction. Release from such constraints might in itself explain the superior individual growth and large increases in population that have been documented for many species in new ranges (Thebaud and Simberloff 2001). When biological control of an invasive species, which involves the deliberate introduction of parasites and predators of the species from its native range, is successful, it is powerful confirmation of the potential role of biotic constraints in curbing a species' abundance and distribution.

In this chapter, we first review the stochastic character of forces that determine the establishment or persistence of populations, especially the small populations that typify immigrants. We then illustrate how biologists have attempted to categorize the role of a population's spatial structure in interacting with the stochastic character. Without attempting to be inclusive, we next proceed to illustrate the breadth of environmental factors, both abiotic and biotic, that form the specific forces that immigrant populations encounter. Finally, we provide illustrations of life-history traits that can influence immigrants' tolerance of a new range. In compiling this chapter, we were aware that some aspects of the discussion of persistence are equally pertinent to the proliferation and spread of a species, the topic of Chapter 4. As a result, we introduce these shared properties or circumstances here and mention them only briefly in Chapter 4. Although additional observations, new hypotheses, and empirical testing are needed to confidently predict the net effect of these countervailing forces on the outcome of a specific species' introduction, a body of data that underlie the basis for establishment is slowly emerging.

STOCHASTIC EXTINCTION— THE PERILS OF SMALL POPULATIONS

The defining demographic of an introduced species is typically its small population. Even the planet's most abundant and widespread invasive species commonly began as "rare" species in their new ranges, compared with the size of their populations in their native ranges. (There are exceptions; see Eckert et al. 1996). Although population extinction can result from deterministic processes—ranging from direct eradication by humans to fire or flooding—a pervasive threat to the persistence of small populations is stochastic extinction. This risk of extinction for small populations transcends the taxonomic groups we examine here. For plants and arthropods, the topic is often examined in terms of the minimal viable population (see Box 3-1); for pathogenic microorganisms, it is referred to as the minimal infective dose. Consequently, our remarks should be interpreted as relevant for all taxonomic groups unless stated otherwise.

Demographic models have relied on such quantities as the mean population growth rate and the variance in growth rate (Leigh 1981, Goodman 1987) and predict that persistence time increases slowly with increasing carrying capacity. As a result, extinction is predicted to be much more likely at lower population numbers, a conclusion that is biologically realistic. To facilitate discussion of the importance of stochastic extinction in the early stages of establishment, the forces

BOX 3-1 Minimal Viable Population

Theoretical development associated with the concept of minimal viable population (MVP) for rare taxa (Soulé 1987, Lande 1988, Menges 1991) has demonstrated the profound demographic implications of low population numbers in the extinction process. Although descriptions of what is implied by MVP have varied (Shaffer 1981), most definitions focus on estimating the minimal population density for a given probability of population persistence over a specified period. In applications of the idea of MVP for rare species, the time frames are often thousands of years (Shaffer 1987). As a result, the recommended population sizes in conservation biology are often large to reduce the likelihood of chance extinction over the long term by various stochastic processes that can differ in their frequency and their potential demographic and evolutionary impacts.

Nonindigenous species are often rare during the initial phases of their colonization. By analogy, an application of the concept of MVP to a newly introduced species might be useful in predicting the likelihood of its establishment. Needed here is knowledge of the acceptable maximal persistence time for the newly introduced species. Precisely because they are at low population densities, new introductions are typically not detected, so it is difficult to know how long they persisted without obvious population growth. However, one would expect that the periods for the establishment phase of currently widespread nonindigenous plants were much less than the 1000-year persistence times sometimes recommended for rare species. Actual periods for the establishment phase in invasive species on which data are available indicate that the initial “lag phase” in the population growth trajectory is often less than 100 years. For example, after initial introduction into northern Australia around 1900, *Mimosa pigra* populations remained small and confined to environs around Darwin until the 1950s. After that short lag phase, this native of Mexico and South America began to spread rapidly throughout Australia’s Northern Territory; it is now a major threat to wetland areas in Kakadu National Park (Lonsdale et al. 1989, Cousens and Mortimer 1995). The population required to ensure persistence for this much shorter period could be very small and thus much more difficult to detect and eradicate. Difficulties in detection because of low population densities might be exacerbated in invasive species that can reproduce vegetatively or by uniparental forms of reproduction. The theory predicts that the population required for persistence of clonal or parthenogenic species is even smaller than those for species that reproduce sexually (MacArthur and Wilson 1967, Shaffer 1981).

Efforts to predict the likelihood of establishment of a recently introduced species will need to consider how an Allee effect may influence the MVP. Life-history traits related to dispersal, reproduction, host finding, predator defense, or other factors can affect the critical density threshold, below which a population that is subject to inverse density dependence cannot recover. Characteristics of the habitat colonized by the founding population can further interact with an Allee effect; the MVP may be higher or lower, depending on the size of the founding colony and the extent of environmental stochasticity.

of stochasticity that can affect population persistence can be grouped into four main categories: demographics, environment, natural catastrophes, and genetics (Shaffer 1981).

Demographic Stochasticity

Demographic stochasticity refers to the chance variation in survival and reproductive rates in very small populations (for example, the probability that all individuals in a population will not reproduce in a given period). Although average values for survival or reproduction might remain relatively constant, chance variation can occur among individuals. As a simple example, consider an annually reproducing population with nonoverlapping age classes, whose average probability of survival to reproduction is 0.20. Despite this average survival rate, if the population is extremely small—say, 10 individuals—there is a probability of about 11% in any one year that all members of the population will die before reproducing, in which case the population will go extinct. If the population is somewhat larger–say, 50 individuals–the probability that the population will go extinct during a given year is very low, less than 0.002%. Equally important is that the probability of demographic extinction is associated with just a single "trial" (that is, a single year). As the "demographic dice" are cast each year, the cumulative probability of chance extinction increases as a simple arithmetic product of the probabilities for all consecutive years if the population does not increase. Although the numerical threshold where demographic stochasticity can cause extinction depends on the particular situation, a threshold estimate for dioecious organisms of about 50 individuals is widely cited (Pollard 1966, Keiding 1975, Shaffer 1981). The fate of a population for which this type of stochastic process becomes important is bleak; as noted by Gilpin and Soulé (1986), demographic stochasticity might well be viewed as "the immediate precursor of extinction."

Environmental Stochasticity

Environmental stochasticity usually reflects the impact of random variation in the environment as it influences a population. In its simplest form, the demographic effects of environmental perturbations are assumed to be equally distributed across all individuals in a particular age or stage class in a population. For example, an increase in seed predators might reduce *average* reproductive output by 80% in a plant population; this decrease, because it represents a drop in average reproductive output across all individuals in the reproductive age class, can severely reduce the size of the population, regardless of its initial size. Because of its capacity to adversely affect even large populations, environmental stochasticity is considered an important force in promoting chance extinction (Sykes 1969, Cohen 1979, Leigh 1981, Menges 1990, 1991). In essence, environmental stochasticity can reduce a population's size to a point at which demographic stochasticity becomes important and causes chance extinction. Goodman (1987) has suggested that when environmental stochasticity is present, expected population persistence time increases roughly as a linear function of population size.

Given that the typical effect of increasing environmental stochasticity is to reduce the likelihood of population persistence, there should be selective value in the capacity of an organism to reduce the demographic impact of environmental variation. One potential evolutionary response is the development of adaptive phenotypic plasticity: reducing the variance in survival, growth, and reproduction buffers the adverse impact of environmental variation on population persistence (Caswell 1983). Because of plants' modular construction, phenotypic plasticity in plant structure has been suggested as an adaptive response to buffer localized gradients in resource availability (Bradshaw 1965, Schlichting 1986). In both plants and animals, physiological plasticity in the form of acclimation to variation in climatic factors, such as temperature, has also been suggested as an adaptive plasticity response (Sultan 1987).

Natural Catastrophes

Floods, fires, earthquakes, droughts, ice storms, and the like, which all occur relatively infrequently and at random intervals, are also potent threats to the persistence of populations. In a sense, natural catastrophes constitute a more extreme and less predictable form of environmental stochasticity. Given the sporadic occurrence of natural catastrophes, it is difficult to characterize the disturbance caused by them and thus incorporate them realistically into models of population persistence. Some theoretical treatments of natural catastrophes indicate that there is a "diminishing-returns" effect: the average persistence time of a population increases only in correspondence to the logarithm of its size (Ewens et al. 1987). Thus, greater and greater increases in population size are required to gain the same increase in persistence time. Further work has indicated that the form of the relationship depends on the carrying capacity of the habitat and on the severity and frequency of catastrophes (Lande 1993). As a result, a population might need to be very large (in the thousands to millions) if it is to persist in spite of periodic catastrophes (Shaffer 1987).

Genetic Stochasticity

Stochastic forces involving founder events, genetic bottlenecks, and genetic drift play a dominant role in determining the fate of immigrant species because frequent colonizing episodes are a central feature of their population biology. These forces tend to dominate during the early stages of establishment after long-distance dispersal, when populations are often very small. Theoretical studies demonstrate that frequent bottlenecks and low effective population sizes reduce genetic variation, especially the frequencies of rare alleles (Nei et al. 1975, Sirkkomaa 1983). However, strong directional selection during the early stages of population establishment can also reduce genetic variation, particularly at loci that govern fitness. Hence, a population early in its postimmigration history is especially vulnerable because random genetic events erode the little genetic diversity that introduced populations usually contain. Low population size can also result in increased mating among related individuals; increased inbreeding can result in the expression of recessive deleterious alleles in homozygous form and cause reduced fitness or inbreeding depression in the progeny (Barrett and Husband 1990, Barrett and Kohn 1991).

The input of mutational variance, recombination, and gene flow theoretically can counteract those forces. In addition, many species have become invaders despite low genetic diversity. In these cases, extensive areas of the introduced range often comprise a small number of genotypes (Moran and Marshall 1978, Scribailo et al. 1984, Barrett and Shore 1989, Novak and Mack 1993). Low diversity at the population and regional levels is especially evident in plant species that propagate by asexual reproduction, sometimes called selfing.

However, effects of genetic bottlenecks associated with introduction of small populations can also be counterintuitive and complex, as evidenced by the introduction of the Argentine ant (*Linepithema humile*) into California. In its native Argentina, intraspecific competition limits colony size and population density, and numerous ant species co-exist with the Argentine ants. Suarez et al. (1999) found that populations of the Argentine ant in California exhibited substantially lower heterozygosity than populations in their native range. Genetic changes in the introduced ant populations were associated with altered behavior that reduced nestmate recognition and hence intraspecific competition and resulted in high population densities, competitive displacement of a majority of the native ant species, and adverse effects on ant predators, such as horned lizards (Suarez et al. 2000). Evidence suggests that the imported fire ant (*Solenopsis invicta*) similarly experienced a pronounced genetic bottleneck when it was introduced into North America (Ross et al. 1993). Altered ecological characteristics and population genetics of the introduced fire ant populations appear to be associated with changes in the social organization of its colonies (Ross et al. 1996). Such changes include multiple queens and zero relatedness between workers and new queens in the introduced populations, compared with few queens and significant relatedness between queens and workers in the native range. Low relatedness has potential advantages for ants and has been associated with rapid colony growth in other ant species (Cole and Wiernasz 1999).

Allee Effects

An Allee effect occurs when low-density populations sustain a zero or even negative rate of increase because of reduced reproduction or survival when conspecifics are insufficiently abundant. Eventually, "undercrowding"—inverse density dependence at low density—drives the population below a critical threshold and extinction occurs (Allee 1931, Courchamp et al. 1999). The dynamics of Allee effects, therefore, can exert a substantial influence on whether a colony of a newly arrived organism is able to persist and become established. One frequent cause of Allee effects is a scarcity of reproductive opportunities at low densities. For example, in some insect populations, difficulty in locating conspecific mates will reduce the likelihood that individuals in the next generation will produce offspring, and in the case of arrhenotokous insects (a population in which unmated females produce only males), will result in a population with a male-biased sex ratio. Ultimately, this form of demographic stochasticity leads to collapse of the population. Other factors may also generate inverse density dependence in low-density populations, including a reduction in the ability of individuals to find or use suitable host plants (Way and Banks 1967), decreased ability to cooperate in defense against predators (Turchin and Kareiva 1993), and genetic inbreeding that leads to decreased fitness (Courchamp et al. 1999, Lamont et al. 1993).

The strength of an Allee effect on the persistence of a population depends on the processes influenced by inverse density dependence. Species in which fitness is enhanced in some way by conspecific facilitation or cooperation may be subject to Allee effects only at very low densities. In contrast, species with obligate sexual reproduction may be more strongly affected by an Allee effect and at a wider range of densities (Courchamp et al. 1999). Species that are subject to a strong Allee effect may also be more vulnerable to extinction due to environmental stochasticity because the population size below which they cannot recover from an unfavorable weather event will be larger than for other species.

Influence of Allee effects on establishment has been addressed by examining the dynamics of populations of nonindigenous species released in biological control programs. Hopper and Roush (1993) found that parasitoid wasp and fly species released for biological control of leaf-feeding insects were subject to an Allee effect when dispersal from low-density populations led to low mating success, which resulted in male-biased sex ratios. Modeling showed that the Allee effect could drive populations to extinction and that it limited establishment of introduced parasitoid species more than the limits imposed by stochastic environmental variation or lack of genetic variation. Grevstad (1999a,b) used simulation modeling to show that if the net reproductive rate of a newly introduced species was even slightly greater than 1.0, demographic stochasticity was unlikely to limit population persistence. Environmental stochasticity, however, interacted with an Allee effect. When an Allee effect was present and environmental conditions were relatively constant, establishment of a species was most likely to be successful if there was a single introduction of many individuals. In contrast, when environmental stochasticity was great, establishment was more likely to occur if there were many introductions of low numbers. Interactions between an Allee effect and environmental variability in larger colonies were more deleterious than the sum of their independent influences; a few years with bad conditions reduced population density to a level where negative population growth eventually led to extinction (Grevstad, 1999a,b). The need to estimate the influence of Allee effects on any immigrant population depends on the species and the circumstance, thereby complicating the population state in a new range.

Effects of Spatial Structure

Models estimating the persistence of a population typically consider only aggregate population statistics, not the spatial distribution of individuals. As a result, the question arises as to whether the extinction dynamics of spatially structured populations (such as a patchy distribution) might differ from those with little spatial structure (such as an aggregate).

The answer is frequently yes. Effects of environmental stochasticity can be reduced if the species is patchily distributed in such a way that not all members in any age class are affected equally by environmental perturbations. The potential for spatial patchiness to function as a buffer against extinctions caused by environmental stochasticity depends, however, on the degree to which environmental fluctuations are correlated across patches (Gilpin 1987, Stacey and Taper 1992). If environmental conditions are correlated across the region occupied by subpopulations of a newly arrived species, "Moran effect" dynamics could lead to a tension between synchronizing effects of extrinsic environmental stochasticity and desynchronizing effects of nonlinear density dependence (Hudson and Cattadori 1999, Ranta et al. 1999). In the Moran effect, originally proposed as a mechanism to explain synchronized fluctuations in Canadian lynx populations (Moran 1953, Royama 1992), when disjunct populations have the same endogenous structure (such as density dependence), a correlated exogenous, density-independent factor (such as weather) will bring population fluctuations into temporal synchrony (Earn et al. 1998, Heino et al. 1997, Hudson and Cattadori 1999, Williams and Liebhold 1995). Thus, when a species is strongly influenced by Moran effect dynamics, a period of unfavorable environmental conditions will promote extirpation of all colonies. A newly arrived immigrant species will persist, therefore, only if at least some subpopulations experience "good times" while other subpopulations suffer reduced population growth during "bad times". In contrast, spatially structured populations may be subject to inverse density dependence regardless of environmental conditions if subpopulations are diluted by dispersal. Such a scenario could increase the probability of extinction due to stochasticity or Allee effects (Hopper and Roush 1993, Lewis and Kareiva 1993).

If the initial distribution of the populations of an immigrant species across a spatial hierarchy is known, this information might predict the potential for spread. The concepts developed in conservation biology for rare native species can be applied to understand the dynamics of the small populations that characterize immigration and establishment. In an attempt to understand what it means to "become rare", Rabinowitz (1981) proposed a classification system that uses three attributes to characterize rarity: local population size, habitat specificity, and geographic range. When expressed as dichotomies, the three attributes result in an eight-cell table (Table 3-1) that describes the spatial characteristics of different forms of rarity. For plant pathogens, *habitat* would refer to the host infected (for example, a wide habitat would mean a wide host range for the pathogen).

The upper-left cell represents the distribution pattern of a common species, but the remaining seven cells describe distinct categories of spatial patterning by which Rabinowitz classified rare taxa and asked questions about the origins of rarity. That approach has application for nonindigenous species: one can ask how nonindigenous species differ in their potential for becoming common. If we assume that immigrants initially consist of small, sparse populations, we can restrict our attention to the bottom row of the table.

Even casual inspection of the categories of the bottom row suggests that some distribution patterns will be more worrisome than others as signals of a species' potential spread in a new range. The far-right cell in the bottom row suggests a single introduction. Because of its habitat specificity and small geo-

TABLE 3-1 Spatial Characteristics of Different Forms of Species Rarity

Local Population Size	Large Geographic Range Habitat Specificity Wide	 Narrow	Small Geographic Range Habitat Specificity Wide	 Narrow
Large, dominant somewhere	Locally abundant over a large range in several habitats	Locally abundant over a large range in a specific habitat	Locally abundant in several habitats but restricted geographically	Locally abundant in a specific habitat but restricted geographically
Small, sparse everywhere	Consistently sparse over a large range and in several habitats	Consistently sparse in a specific habitat but over a large geographic range	Consistently sparse in several habitats but restricted geographically	Consistently sparse in a specific habitat and geographically restricted

SOURCE: Adapted from Rabinowitz 1981.

graphic range, this type of immigrant is probably most susceptible to stochastic extinction. At the other end of the spectrum is the immigrant described by the far-left cell in the bottom row. This species inhabits a broad geographic range and is found in many habitats (or associated with many host species). Its wide distribution (both geographically and by type of habitat) might reflect multiple introductions. Stochastic extinction is very unlikely for a species with this distribution pattern. Obviously, if populations increase in size (move to the upper row), the species will become common and probably invasive. The next cell to the right represents a scenario that, again because of the broad geographic range, suggests multiple introductions. Because the species is restricted to a particular habitat, the emergence of an invader through this scenario might be predictable, and effective management and containment of the species might be quite feasible.

Rabinowitz (1981) suggested that there might be no rare species in the last category (third cell, second row). There might indeed be no rare native species that are limited geographically and are found at low population density in several habitats. However, this scenario could be common among persistent nonindigenous species. It represents a situation similar to that of the most problematic category (the far-left cell) except that the limited geographic range described for this cell suggests a single introduction. One might suspect that such a species could become established, and even invasive, and is limited only by lack of additional introductions throughout its potential range. Early detection of a nonindigenous species with this distribution should evoke immediate consideration of eradication.

Although those categories are admittedly simplistic, they do provide a general conceptual framework for understanding the various pathways to abundance that a newly established immigrant population might follow.

Avoiding Stochasticity: Multiple Introductions and Population Size

Aside from the obvious inability of a population to survive under a climatic regimen that is well beyond its tolerance, stochasticity is the greatest threat to small populations. And as stated above, small numbers typify most unintentional introductions of nonindigenous species. But if the founder population is large enough or replenished with additional propagules, it can withstand stochastic forces—provided it can tolerate the overall character of the new environment.

Empirical studies of the relationship between the probability of establishment and the size of the founding population stem from evaluations of efforts to establish insects for biological control. In general, establishment is predicted to increase with population size (Grevstad 1999a). However, it is also possible that persistence is independent of population size if density-independent factors—such as weather, habitat conditions and the size of the habitat patch—are the main determinants of persistence or if the population's numerical increase allows initially small populations to escape rapidly the risk of extinction.

Bierne (1975), in a widely cited retrospective analysis of the role of initial colony size in establishment, reviewed Canadian biological control programs. He found that if fewer than 5000 individuals were released, about 9% of the species became established—a percentage that is similar to the 10% estimated for accidental introductions (Williamson 1996). If at least 30,000 individuals were released, 79% of the species became established. The average number of individuals per release site also seemed to be important; establishment rates increased from 15% to 65% of species if at least 800 individuals were released at a single location. Bierne's (1975) approach has limitations: the role of the number of individuals released in each case might be confounded by the traits of particular species; and these traits also contribute to establishment, such as a high reproductive rate or abundant distribution in their native range (Crawley 1986, 1989b). Grevstad (1999a) took an experimental approach in assessing relationships between population size and persistence. She followed the fate of 92 experimental releases of two chrysomelid beetles for three full generations and found that the probability of establishment increased over the range of initial beetle density (20, 60, 180, and 540 beetles). Population growth rates varied among environments but were positively related to release size. In a second experiment, in 20 releases of single gravid females, only one female founded a population that persisted for the duration of the 3-year study.

Although Levine and D'Antonio (1999) contend that any community, given enough propagules, can be invaded, nonindigenous insects are usually introduced accidentally and presumably arrive in low numbers in most cases. Small populations have a greater random chance of extinction than large populations and are more vulnerable to inbreeding depression, so the descendants of founders might also need propitious conditions to survive. Liebhold et al. (1995) and MacArthur and Wilson (1967) suggest that the probability of establishment can be simply described as a continuous function of initial population size. Translating these conclusions into practical terms is currently difficult because the small immigrant population that is detected may be only one of a large group of small populations that arrived at the same time. Although many may soon go extinct, some may survive unless they are deliberately eradicated.

Not only a large number of immigrants per introduction, but also frequent introductions will mitigate stochastic processes and increase the likelihood of establishment. Crawley (1986) found that the probability of establishment increased with both the sizes and the number of population releases. Repeated introductions increase the chance that an immigrant species will encounter a combination of resources, scarcity of competitors, and low density of predators or pathogens that will permit establishment. That expectation appears to be borne out in the release of insects for biological control. In the Canadian biological control programs, nonindigenous species that were released in at least 10 episodes established in 70% of the cases; those released in fewer than 10 episodes established in only 10% of the cases (Bierne 1975).

Simulation analyses using matrix models can examine how such factors as environmental stochasticity can interact with demographic characteristics, such as deterministic growth rate (λ), to influence the persistence of small populations. Using stage-structured matrix models, Menges (1990, 1991, 1992) explored how the persistence of plant populations is affected by environmental stochasticity and how the effects of environmental stochasticity are modulated by variation in rates of increase. Using life-table data on several plant species, Menges (1992) found that, except for very small populations with deterministic growth rates near 1.0, demographic stochasticity was much less important than environmental stochasticity in causing chance extinction. Moderate environmental stochasticity was found to cause extinction even in populations with positive deterministic growth rates. By systematically varying environmental stochasticity in a series of simulations, he demonstrated that populations with deterministic growth rates near 1.0 are much more likely than populations with higher growth rates to go extinct when exposed to moderate environmental stochasticity. Populations with deterministic growth rates greater than 1.2 were affected only by extreme environmental stochasticity. The potential importance of that final result to invasion biology is that if the deterministic growth rate of a newly established population of invaders is much greater than 1.0 (say, 1.5 or higher) the likelihood of chance extinction is much reduced.

THE ENVIRONMENTAL CONTEXT

Against the continuous backdrop of stochastic forces that affect a fledgling population are the environmental characteristics of the new range. Abiotic factors–such as climate and landscape–will determine whether a new range is at least minimally habitable by an immigrant. Biotic factors–including the availability of hosts or pollinators and the presence of competitors, predators, and plant-pathogen antagonists–challenge the biological tolerance and competitive abilities of the newcomer. The following discussion is by necessity abridged and serves only to illustrate the breadth of environmental factors that affect establishment.

Abiotic Factors

The likelihood of establishment will be affected by the general climatic match between the donor habitat and the new habitat of the immigrant species. Moreover, the geographic distribution and range of climatic conditions known to have been suitable for the immigrant species in its native range or in previously invaded regions provide some indication of potentially suitable habitats. Prediction of establishment and invasiveness based on climate-matching between original and potential ranges of nonindigenous species is a subject of active research (Kriticos and Randall 2001). This correspondence is related to the potential inability of a nonindigenous species to tolerate weather and climatic conditions in a new range, a common cause of founder-population extinction (Crawley 1986, Leigh 1981, Levins and Heatwole 1973).

In addition, the latitudinal range can affect the ability of many species to become synchronized rapidly with a new habitat. Insects in a new range must initiate and terminate diapause at appropriate times to cope with climatic extremes. If we consider insects in the Northern Hemisphere, we might expect that insects from northern latitudes would be more likely to become established in southern latitudes of the Northern Hemisphere than the reverse. The higher probability of establishment in southern latitudes occurs because the consequences of failing to enter diapause soon enough in autumn or breaking diapause too early in spring are presumably more detrimental than entering diapause too early or breaking it relatively late. Niemelä and Mattson (1996) noted that deciduous forests in Europe span a higher latitudinal range (43-60°N) than deciduous forests in the United States and Canada (30-48°N); this might partially explain the invasion of many European forest insect species in North America.

Similarly, establishment of univoltine insects (those with only one generation each year) would be unlikely if an insect moved between the Northern Hemisphere and the Southern Hemisphere. Such a species would be disadvantaged because dormant eggs or pupal stages would encounter antipodal seasons in the new habitat (Simberloff 1986, Ridley et al. 2000).

For introduced forest pathogens, temperature and moisture appear to be critical. The influence of climate on the incidence of plant disease incidence has been studied for those indigenous and nonindigenous microorganisms that exist in the United States and infect agricultural crops (Coakley 1988). Numerous climatic factors, particularly moisture and temperature, dictate where a microbe survives and whether it is able to infect a suitable host. Predictive models, based in part on climatic factors, have become increasingly useful in estimating disease severity and showing patterns of potential pathogen distribution on crops, for example, with *Peronospora tabacina,* the tobacco blue mold (Main et al. 1998).

Damage by the introduced European larch canker organism (*Lachnellula willkommii*) appears restricted to the coasts in eastern Canada and Maine (Ostaff 1985), where fog, more rainfall, less snow, and higher mean monthly winter temperatures than inland sites are prerequisites for disease development. With Scleroderris canker, another disease of conifers, the introduced European race of the causal fungus, *Ascocalyx abietina*, predominantly infects seedlings and lower branches of some pine species. As with the North American race, a period of low temperatures and snow appears necessary for the disease to develop (Marosy et al. 1989). As a result, this pathogen has not spread substantially beyond the sites where it was introduced on infected nursery stock in Canada and the United States (Laflamme et al. 1998). *Cronartium ribicola,* the introduced pathogen responsible for white pine blister rust, has been the object of one of the more detailed evaluations of microclimatic factors that constrain infections. Higher infection rates occur where air drainage influences spore dispersal and provides the specific microclimatic conditions required for infection (Van Arsdal 1967, Dahir and Cummings Carlson 2001).

To understand how variation in the physical environment might affect immigrant populations, it is critical to relate the environment to demographic characteristics. For example, even if the average climatic conditions at a site favor population growth and persistence in most years, variation around the average growth rate caused by an occasional year of unfavorable weather can drive the population to extinction. Weather, the combined random variation in a host of climatic variables, is often the primary source of the environmental stochasticity incorporated into population viability analysis. Extreme weather events are one aspect of this stochasticity. Thus, a species from a native range without extreme weather events could conceivably be at heightened risk in a potential new range simply because of the occurrence of this expression of stochasticity.

Although the importance of human-generated disturbance in promoting the spread of invaders is well established (Harper 1965, Mack 1989), the role of disturbance in affecting the early establishment of invasive species is uncertain. Disturbance can reduce an immigrant population to such a low density that demographic stochasticity could cause extinction. It can also adversely affect population persistence if it increases environmental stochasticity or takes the form of natural or human-mediated catastrophes.

However, if disturbance effectively reduces environmental stochasticity or increases resource availability or both, it can promote the persistence of the initial colonists. A common example of this type of enhancement of population persistence by disturbance is cultivation. Plant cultivation typically reduces seasonal and year-to-year variation in a wide array of environmental factors, both abiotic and biotic. In addition to reducing variation in demographic characteristics, the higher level of resource availability typical in cultivated systems increases average population growth and further decreases the impact of environmental stochasticity on population persistence. By reducing environmental stochasticity and eliminating native competitors, cultivation can be a potent force in promoting the persistence of nonindigenous populations, thereby eventually allowing them to become established and even invasive (Mack 2000).

Biotic Factors

Native organisms in the new range of a recently introduced species can be essential for its survival as hosts, mutualists, and vectors, or they can threaten its survival as predators, grazers, competitors, parasites, and pathogen antagonists. The consequences of these agents might not be expressed on entry of the immigrants into the new range. Strong et al. (1984) showed that the likelihood that a nonindigenous species will encounter such new biotic constraints depends on the length of time in the new range, the size of the new range, and the availability of nonindigenous enemies. That an immigrant species will eventually acquire new biotic constraints seems inevitable, although the constraints might not arrive until long after the nonindigenous species has become persistent or even invasive (Strong et al. 1984).

A multitude of biotic factors can prevent establishment of immigrant insects and pathogens in a new range. The immigrants must be able to locate suitable host plants or come into contact with a suitable host through the deposition of spores and eggs or other dispersal units, survive interactions with newly encountered enemies, and compete with native species. A new nonindigenous insect or pathogen is often not detected for years or even decades (Carey 1996), and the difficulty of early detection makes it difficult to identify factors that were conducive to establishment. General patterns can be recognized, however, and might be useful in efforts to predict future invasions.

Host Availability and Distribution

The establishment of nonindigenous pathogens and arthropods is subject to the availability of a suitable host. Some plant pathogens, such as the cereal rust fungi, are extreme specialists; they infect only specific plant varieties. Others—for example, such root pathogens as *Pythium* species, will infect a wide taxonomic range of hosts. Although the wide host compatibility of some pathogens increases the probability of their finding a suitable host, many pathogens with narrow host ranges (such as *Sporisorium sorghi*, the sorghum smut fungus) have become established and even invasive in the United States. For example, plant pathogens that have invaded the temperate forests of North America cause epidemics on a few closely related species. Generalist pathogens are rare in forest ecosystems; one example is *Erwinia amylovara,* the fire blight pathogen (Vanneste 2000).

Not surprisingly, North American forests have been invaded by pathogens from areas with similar hosts and climates. But the long-term isolation of the North American forest flora from floras that are the source of pathogens might predispose the forests to invasion because susceptible genotypes could have evolved in the absence of pathogens that would have constrained their survival (von Broembsen, 1989).

Pathogens of minor significance in one location can cause epidemics when transferred elsewhere. For example, races of the stem rust pathogen *Puccinia graminis* were blown from moderately resistant wheat varieties in Australia to highly susceptible ones in New Zealand (Watson 1970). A most noteworthy example in the United States is the recent identification of the fungus *Phytophthora ramorum*, which has been associated with the disease, sudden oak death. Its hosts in California include oak and numerous other plant species. Although the origin of the fungus is not known, it was probably introduced and is known to cause a leaf spot and dieback of rhododendron in Europe (California Oak Mortality Task Force 2001).

There is a close genetic relationship between pathogens and their hosts. Many plant pathogens contain avirulence genes that trigger defense responses in plants that have corresponding resistance genes. In the absence of one or both corresponding genes, the pathogen escapes recognition and is able to replicate to high levels (Keen 1990). Information about the regional distribution of pathogen populations and the frequency of different avirulence genes in those populations can be important predictors of whether a host plant species will be available (susceptible) or not (resistant). If the virulence or avirulence of a potential invading pathogen is known, the vulnerability of a plant species can be predicted rather accurately (Mekwatanakarn et al. 2000).

The likelihood of establishment of nonindigenous, phytophagous insects depends critically on the availability of host plants that foster larval development and other life stages. Crawley (1986) analyzed establishment of insects released for the biological control of nonindigenous plants and concluded that the most common reason for their failure to establish was insect-plant incompatibility. Similarly, Barbosa and Schaefer (1997) suggested that abundance of invading herbivorous insects depended primarily on the availability and quality of host plants.

The trans-Atlantic establishment of insects is facilitated by the high degree of similarity between North American and European hosts in structural, biochemical, and spectral properties (Fraser and Lawton 1994, Jones and Lawton 1991, Niemelä and Mattson 1996). That conclusion is based on the assumption that immigrant species are conservative and are less likely to attack plants that are taxonomically or chemically distinct from their native host plants. Therefore, the degree of taxonomic difference between host plants in the native range of a nonindigenous insect and potential host plants in a new habitat could be a useful predictive tool (Strong et al. 1984, Niemelä and Mattson 1996). Most European forest insects that have become established in the United States attack the same tree genera in the United States that they attack in Europe (Mattson et al. 1994). Niemelä and Mattson (1996) found that North American trees that supported the highest numbers of European invasive insects were well represented at the genus or family level in Europe; trees peculiar to North America (such as *Robinia pseudo-acacia*) support few European insects.

The fact that more European insects have invaded North America than the reverse could also reflect the diverse flora of North America that includes many European plants and the relatively high rate of plant extinctions in Europe. The total vascular plant flora of North America is composed of roughly 18,000 species, including 16 genera and 97 species of gymnosperms and 143 genera and 503 species of angiosperms. In comparison, there are about 12,000 vascular plant species in Europe, including eight genera and 30 species of gymnosperms and 78 genera and 256 species of angiosperms (Niemelä and Mattson 1996 and references therein). At least 20 tree genera are extinct in Europe but are still found in North America. The high numbers of congeneric and confamilial plant species in

North America presumably made it relatively easy for immigrant European species to find suitable hosts on this continent. Niemelä and Mattson (1996) have speculated that insects that relied exclusively on plant hosts that are now extinct are themselves extinct if they could not attack a confamilial relative.

Diet breadth of a nonindigenous insect is important in assessing host availability. Nonindigenous insects that are capable of feeding on a wide variety of hosts often can forage on novel hosts in their new range. Therefore, insects that are able to use many species as hosts in their native range could be less reliant on locating plants in a new range that are similar to their native diet; this lack of specificity could facilitate establishment. Simberloff (1989) pointed out, however, that the assumption that broad diet breadth confers ecological versatility and hence higher success rates for nonindigenous insects of this type is not always reflected in empirical data. For example, various insects that became established in biological control programs were often intentionally chosen for their high degree of host specificity.

Niemelä and Mattson (1996) classified tree-feeding insects of European origin that are found in North America as monophagous, oligophagous, or polyphagous, depending on whether they fed on one genus, more than one genus in a single family, or more than one family of plants, respectively. Of the nearly 400 European invaders in North America, 68% were found to be monophagous or oligophagous, and the remaining 32% were polyphagous (Mattson et al. 1994, Niemelä and Mattson 1996). It is not clear, however, whether this pattern indicates that specialized feeders are more likely to become established than generalists or that there simply were more opportunities for invasion of specialized feeders. A random sample of the British insect fauna found that 75% of plant-feeding insects were monophagous or oligophagous, and 25% were polyphagous (Bernays and Chapman 1994). If the British fauna are representative of broad patterns across Europe, invasion by polyphagous insects may be about as likely as for monophagous species.

The relation of diet breadth to host availability may have implications for nonindigenous herbivorous insects originating in other regions, such as Asia. Insects with specialized diets may be less likely to become established in a new area than insects with broad diets because they are less likely to encounter acceptable hosts. The contrast that emerges from a comparison of diet breadth of forest insects originating in Europe and Asia appears to support this hypothesis. Mattson et al. (1994) compiled host-plant and origin data for 266 forest insect species established in North America that are native to Europe and 68 species that are native to Asia. More than 50% of the Asian species were polyphagous, but, as cited above, only 32% of the European species were polyphagous. The higher degree of polyphagy characteristic of the Asian invaders may reflect lower overall floristic similarity between trees in Asia and North America than between trees in Europe and North America. This observation depends heavily, however, on the regions being compared: temperate China's mesophytic forests share a striking similarity to tree genera in North America (Axelrod et al. 1998 and references therein). Although data on other groups of nonindigenous insects should be examined, the pattern suggests that polyphagy is most likely to favor establishment when the flora in a new range differs substantially from the flora in the immigrant insect's native range.

Spatial distribution and abundance of potential hosts affect the ability of a nonindigenous insect to locate suitable hosts and the probability that a pathogen will come into contact with a susceptible host (MacArthur and Wilson 1967, Shigesada and Kawasaki 1997). A host with a patchy or fragmented distribution might be less likely to be colonized by a nonindigenous species, or its distribution could reduce the movement among local populations of a nonindigenous species and thereby lead to a greater chance of extinction than a host that is abundant or continuously distributed. A patchy host population can also reduce the rate of increase of pathogen or insect populations (Hughes et al. 1997). For example, one factor that might partially account for the order-of-magnitude higher number of European forest insects established in North America than the reverse is the lower total area and less continuous distribution of European forests than of forests in North America (Niemelä and Mattson 1996). In Britain, Fraser and Lawton (1994) reported that more than 2% of the European moths that originally fed on angiosperms have begun feeding on conifers. They suggested that a continent-wide conifer afforestation program in Europe has been a major factor in this host-range extension.

Abundance and distribution of host plants may also be related to how Allee effects influence a low-density population of a newly introduced species. If individuals of a founding population must disperse widely to find suitable hosts, founding populations may be "diluted" to even lower densities. Inverse density dependence arising from reduced reproductive success or poor survival at low densities may lead eventually to extinction (Courchamp et al. 1999). Life-history traits, such as aggregation pheromones or the ability to detect host volatiles, should enhance the ability of a newly introduced species to effectively locate a suitable host. Presumably, such traits should increase the probability of establishment, although empirical tests of this assumption are lacking.

Hosts must be available to immigrant arthropods and pathogens temporally, as well as spatially. In other words, a nonindigenous arthropod must rapidly establish phenological synchrony with its potential host plants in a new range (Quiring 1992, Wood et al. 1990). Establishment of an immigrant arthropod or pathogen might be facilitated by host plants that are distributed across a wide range of latitudes or elevations and by multiple introductions of the arthropod or pathogen during the year. Insects that use endophytic cues, such as oviposition within plant tissues, might more readily synchronize with the phenology of their hosts (Wood et al. 1990). Synchronization with hosts enables insects to take advantage of ephemeral peaks in nutrient availability or foliage quality and could also promote temporal synchronization of mate-finding or dispersal (Wood et al. 1990).

Natural Enemies

Typically, nonindigenous plants, insects, and pathogens that are accidentally introduced into a new range arrive without the complement of natural enemies—such as predators, parasitoids, parasites, antagonists, and pathogens—with which they interacted in their native range. Whether native species can expand their diet to include the immigrants and whether the newly encountered enemies will prevent establishment of the nonindigenous species are important questions.

Establishment will be less likely if the intrinsic rate of increase (r) of the immigrant is small, if the immigrant is particularly vulnerable to attack by resident enemies, or if populations of resident enemies are large (Lawton and Brown 1986). The likelihood that native enemies will exclude a nonindigenous species presumably depends on the numbers and densities of the potential predator and pathogen species, their feeding preferences, and the total number of native prey species that are of higher preference than the immigrants (Crawley 1986). All together, the more similar an immigrant species is to a native species, the more vulnerable it will be to native enemies, because the rate of attack should be high (Lawton 1990).

The likelihood that predators or other enemies in the new range will prevent establishment of a nonindigenous insect could also be influenced by the structure of the predatory "guild" in the community. Pimm (1989) suggested that when predation exerts a strong influence on prey species, an immigrant species would have more difficulty becoming established in a community with a single predator than one with several predatory species. He based that suggestion on observations of a close correlation between predator and prey species in communities with various numbers of species (Jeffries and Lawton 1984) and the assumption that the correlation reflects the influence of predators on numbers of prey, as well as the reverse.

Evidence of the ability of indigenous species to prevent establishment of nonindigenous insects in its new range is scarce, and the topic deserves much further research. Much of the evidence stems from postrelease evaluations of herbivorous insects introduced for biological control. Goeden and Louda (1976) assessed impacts of resident predators, parasitoids, and pathogens on nonindigenous herbivorous insects introduced for biological control in 23 projects. Effects of resident natural enemies varied widely; there was no discernable impact on the introduced species in five to nine projects, there was some adverse effect on the introduced species in 12 to 17 projects, and establishment was prevented in two projects.

In postrelease evaluations of biological control releases of insects, impacts of predators were generally greater than impacts of parasitoids or pathogens. Goeden and Louda (1976) concluded that invertebrate predation, mostly by insects, sometimes had substantial impacts on the fate of introductions, whereas effects of vertebrate predators were generally minor and localized. Indigenous predators that prevented establishment or had a measurable impact on the introduced species were usually polyphagous. Effects of predators on introduced herbivorous species did not seem to be affected by whether the herbivore was an endophagous or ectophagous feeder, whether its mouthparts were haustellate or mandibulate, or whether the herbivore was univoltine or multivoltine. In one notable case, native insect predators prevented establishment of cinnabar moth (*Tyria jacobaeae*) when it was introduced into Australia to control ragwort (*Senecio jacobaea*). Insect and bird predation also prevented its establishment in New Zealand (Goeden and Louda 1976, Lawton and Brown 1986). Goeden and Louda (1976) found no examples of deliberate insect introductions that failed to establish because of indigenous parasitism or pathogens, although these enemies sometimes limited the growth of immigrant populations after establishment. Most parasitoids that had a discernable effect on a nonindigenous species transferred from a native host that was related to the target host at least at the family level. Endophagous herbivores, primarily mandibulate species, were most often attacked by resident parasitoids. Samways (1979) reported that when a sphingid moth entered an experimental plot of cassava in Brazil, resident egg and larval parasitoids prevented any moth larvae from completing development.

If resident enemies are more likely to prevent establishment of a nonindigenous species that is similar to their native prey, the converse prediction is that establishment should be more likely for species that are different from native prey species (Lawton and Brown 1986). Lawton and Brown (1986) suggested that the rapid invasion of Britain by the cynipid Knopper gall wasp exemplifies this prediction. That the Knopper gall wasp apparently has no morphologically similar native counterparts on British oaks appears to account for the inability of indigenous natural enemies of gall wasps to locate or attack it. Similarly, adelgid insects, a group of sap-feeding insects that infest conifers, have no known parasitoids in North America. That could account at least partially for the successful invasion of nonindigenous species, such as hemlock woolly adelgid and balsam woolly adelgid. The degree of taxonomic relatedness could also be important in explaining the ability of nonindigenous plants to become established in new ranges where they lack native relatives (Mack 1996b).

The limited evidence available suggests that the potential influence of resident enemies on newly arrived populations of nonindigenous insects is difficult to predict. Lawton and Brown (1986) noted that Holt's (1977, 1984) models to predict the outcome of an introduction require knowledge of the abundance of the various potential enemies of the immigrant, estimates of their attack rates, and the rate of increase of the immigrant. Adequate information for predicting how natural enemies will influence an introduction is not likely to be available before or just after the immigration. They also pointed out that it is generally much easier to understand retrospectively the circumstances that led to an invasion than to predict the outcome of any particular case–a conclusion with which the committee concurs and sees as applicable to the whole issue of establishment.

Nonindigenous pathogens can also face "enemies". Populations of native leaf epiphytes or endophytes or natural communities of soil microorganisms that suppress native pathogens might also serve as antagonists to the establishment and spread of nonindigenous pathogens (Cook 1993). These microbial antagonists range from bacteria to mycoparasites. A unique group of hypoviruses has enabled substantial biological control of chestnut blight in Europe and Michigan (MacDonald and Fulbright, 1991). When virulent strains of *Cryphonectria parasitica* are infected with the hypoviruses, their ability to infect chestnut and reproduce is typically reduced; they become hypovirulent. The hypoviruses appear to have their origin in eastern Asia with their fungal host (Peever et al., 1998). Hypoviruses or their genetically modified variants eventually may prove useful as biological control agents for chestnut blight within chestnut's native North American range (Dawe and Nuss 2001). Similarly, mycoviruses (called "d-factor") that correlate with the presence of multiple dsRNA segments in the Dutch elm disease fungus, *Ophiostoma novo-ulmi* may attenuate the pathogenicity of the fungus. However, their overall effect on the dynamics of Dutch elm disease is unclear, as is their potential use as biological control agents (Brasier 1990).

Predators of seed and vegetative tissue cause immediate death of a plant immigrant. Seed predators can be particularly effective because plant immigrants are most likely to arrive as seeds, and of course seed production is likely to be crucial to the immigrants' persistence in the new range. Ants, for example, have apparently blocked the establishment of some nonindigenous tree species in the Caribbean region (Little and Wadsworth 1964). But the list of seed predators is by no means restricted to ants or even insects; rodents can be such voracious seed predators of *Cakile maritima* that it has been prevented from expanding its range locally in California. Predation of nonindigenous plants, apart from seeds, has commonly involved seedlings. Again, the plants are characteristically small and unable to withstand even a single attack (Mack 1996a).

The action of grazers–organisms that remove plant material in one or more nonlethal events–can be cumulative to the point at which the plant dies outright or dies from the infections that grazing can facilitate. Some termites, which as a group characteristically attack only dead wood, can attack living wood. Their attacks have been so severe for some nonindigenous plants as to thwart their establishment. Eucalypts, which are native to Australia and New Guinea, have been prevented from establishing in some locales in Brazil and West Africa by chronic termite grazing. And grazing can contribute indirectly to extirpation by reducing the ability of immigrants to survive competition or parasitism (Mack 1996a).

Perhaps the most frequent biotic constraint imposed on plants in a new range has been attack by pathogens. There are spectacular examples in which a nonindigenous plant species has been destroyed by an indigenous parasite. In such cases, establishment or naturalization is out of the question. The fate of cacao in West Africa is illustrative. Cacao (*Theobroma cacao*) is native to the Amazon Basin. It is successfully cultivated in West Africa but only if scrupulously protected from the cacao swollen-shoot virus (CSSV), an indigenous virus in West Africa that attacks native West African relatives of cacao. A native scale insect serves as the vector of the virus. Cacao, which has no natural resistance in cacao to CCSV, can be cultivated in West Africa only as long as movement of the scale insect from tree to tree is diligently prevented and a quarantine and destruction protocol for infected trees is rigidly enforced (Jeger and Thresh 1993). A further example of host range extension of an endemic pathogen to a nonindigenous plant species is now occurring in the United States. Multiflora rose (*Rosa multiflora*) was advancing unchecked in its range expansion across the United States from east to west until it came into contact with native roses infected by rose rosette disease (RRD). This endemic disease is caused by a yet uncharacterized agent that is transmitted by a native mite (*Phyllocoptes fructiphylus*). Because RRD is highly pathogenic to multiflora rose, the incidence and impact of multiflora rose is diminishing in many midwestern and eastern states (Epstein and Hill 1999).

Those examples involve spectacular action by resident pathogens, but we do not know how often such phenomena occur. Some generalist parasites thwart establishment of nonindigenous species. Texas root rot fungus, *Phymatrotrichum omnivorum,* is a generalist soil parasite that has remained indigenous in the U.S. Southwest and adjacent Mexico. It attacks at least 2000 plant taxa in more than 40 families and is highly virulent in many of these hosts. The parasite attacks so many nonindigenous woody ornamentals that it is a major deterrent to the introduction of woody horticultural species in the Southwest. Some species, such as *Ulmus americana,* will not persist in the range of Texas root rot, because of their vulnerability to it (Mack 2002).

Competitors

Hypothetically, establishment of nonindigenous insects could be affected by interference or exploitation competition with resident species. In interference competition, one species reduces the fitness of another through an action, such as fighting or allelopathy, that is not directly related to resource availability or abundance. Exploitation competition occurs when the rate of resource availability or supply determines the rate of change among populations of different species. Resource availability to the immigrants will depend on the standing crop of the resource (which is a function of the feeding behavior of resident competitors), the productivity of the resource, and the rate at which the resource is removed by the resident competitor (Crawley 1986). Immigrants should have a greater probability of establishment if the rate of resource availability is adequate or the number of competitors is low enough to permit the immigrant population to be maintained. Crawley (1986) proposed that when insect guilds are structured by interference competition, invasion by a larger or fiercer species is more likely. Conversely, a small species could more likely become established within a guild structured by exploitation interference in which it can reduce the resource supply rate to the point where larger, resident species can no longer be supported.

Although those predictions are intuitively appealing, it is difficult to find situations where competition with native residents has directly affected establishment of nonindigenous insects. Levins and Heatwole (1973) introduced a *Drosophila* species, an ant, a snail, frogs, and lizards to a small Puerto Rican island. The *Drosophila* species, the frogs, and the snail went extinct rapidly because of severe weather. The introduced ant and lizards survived for a while but eventually went extinct. The authors attributed extinction of the ant to competition with aggressive native fire ants and extinction of the lizards to competition and predation by resident species.

Introductions of herbivorous insects for the biological control of nonindigenous plants often provide little information, because interspecific competition is, by careful prerelease evaluation, minimal in such situations. Some have noted that the populations of entomophagous species for biological control introduced earliest are more likely to establish than populations introduced later (Tallamy 1983, Ehler and Hall 1982). In some cases, that outcome could reflect competitive exclusion of later introductions by previously established species. A more probable explanation, however, is that the order of species' introductions is determined by the expectations of those importing the species; that is, biological control practitioners attempt to establish the species that are most likely to be rapidly successful (Keller 1984, Simberloff 1989).

How and whether competitive abilities influence establishment of nonindigenous insects have attracted much speculation, particularly with respect to asymmetry in the establishment of insects between two regions or countries. Vermeij (1991) proposed that the prevalence of asymmetrical exchanges of species between regions could be related to differences in the competitive abilities of immigrants originating in different donor ranges. European insects, for example, have disproportionately invaded other regions (Crosby 1986, di Castri 1989, Niemelä and Mattson 1996, Simberloff 1989). Niemelä and Mattson (1996) speculated that climatic and anthropogenic disturbances in Europe shaped selection for suites of traits likely to enhance the survival of insect species in the fragmented and impoverished European forests. A lower ratio of phytophagous insect species to plant species compared with the ratio on other continents might have also intensified interspecific competition in Europe. European plant-feeders that arrive in a new range, therefore, might be inherently strong competitors. That hypothesis would obviously be difficult to test empirically, and the explanation is almost certainly confounded by differences in the number of opportunities for transport (Simberloff 1989). However, the much larger number of European forest insects established in North America than the reverse—despite historical movement of plant material, lumber, and other products from North America to Europe (Niemelä and Mattson 1996)—is consistent with such a pattern. Simberloff (1989) addressed the general assumption that islands are more frequently invaded by mainland species than the reverse because mainland species are superior competitors. He pointed out that the available data, which are primarily from agricultural systems, do not support that assumption. The relatively frequent invasions of islands by mainland species could instead reflect the greater abundance of mainland species or the greater frequency of opportunities for invasion of islands by mainland species. Moreover, although competition had been documented for some guilds of insects, such as ants (Suarez et al. 1999) and pine phloem-feeders (Light et al. 1983, Poland and Borden 1998), evidence of interspecific competition among foliage-feeding and sap-feeding insects is scarce (Denno et al. 1995, Strong et al. 1984).

Plant competitors can locally extirpate an immigrant population of plants. The evidence has been indirect–the abandonment of a commercial planting because competition by native plants was so severe and pervasive that cultivation alone was insufficient to foster plant establishment. Several native vines apparently prevent the establishment of introduced tree species in the Solomon Islands (Neil 1984). Competition for light probably produces many more cases of such biotic constraint among nonindigenous species, although no specific search for examples has yet been attempted. Closed-canopy forest communities in the United States, dominated by angiosperms or conifers, have much lower numbers of naturalized species than the same sites once the canopy is removed. For example, although the naturalized and adventive flora of New England probably exceeds 800 species (Seymour 1982), few (for example, *Ailanthus altissima*) are naturalized in New England forests. The rest occur only in undisturbed open communities and in forest habitats in which the canopy has been removed, such as sites logged or long held in cultivation. Although shade would not provide a strong barrier to nonindigenous species that are shade-tolerant, shade-tolerant species either have been introduced infrequently or, more likely, other physical or biotic factors have so far constrained their establishment. Nevertheless, nonindigenous shade-tolerant species constitute a functional category of species whose careful monitoring appears warranted upon their introduction in the United States.

Another difficulty in addressing how competition affects establishment arises because we cannot necessarily distinguish between effects of natural enemies and of competitors when a nonindigenous species arrives. An immigrant species and a native prey species can exhibit “apparent competition” through a shared enemy—a concept similar to the competition for enemy-free space described by Jeffries and Lawton (1984). The outcome of such competition can depend on r, the intrinsic rate of increase of the immigrant, and the rate at which the nonindigenous species is attacked by resident enemies (Holt 1977, Lawton and Brown 1986). Establishment should be more likely when r is high, but interactions between the diet breadth of the native predators and the specificity of their foraging niche make it difficult to test this hypothesis (Lawton and Brown 1986).

Vectors and Mutualists

Some pathogens are transported by insect vectors to potential hosts (Nault 1977, Harris and Maramorosch 1980, Tolin 1991) and a dramatic increase in the incidence of a disease, whether caused by a native or nonindigenous pathogen, can indicate the arrival of a nonindigenous vector. For example, *Xylella fastidiosa*, the bacterial agent of Pierce's disease, has been known to occur in vineyards in California since the 1800s and is transmitted by leafhoppers, but the recent arrival of the glassy-winged sharpshooter (*Homalodisca coagulata)*, which feeds on several other important hosts (including almond, citrus, alfalfa, and oleanders), has dramatically increased the potential threat of Pierce's disease to the agricultural industry in California (Purcell 2000). The abundance, spatial distribution, and temporal availability of the vector can, therefore, affect pathogen establishment.

Nonindigenous plants are autotrophs, but their ability to establish can depend on the presence of another species, a mutualist, in the new range. Mutualists are pairs of species for which association brings mutual benefit. In the context of nonindigenous species' entry and survival, only one or neither species may be native to the new range (Simberloff and Von Holle 1999, Richardson et al. 2000). The scenarios by which this dependence can occur are well known and begin with the absence of an obligate pollinator. For example, nonindigenous *Ficus* species, each of which requires a single species of wasp for pollination, were not deemed threats to establish in the United States until the obligate pollinators for three of the species were detected in southern Florida in the 1990s. Seedlings have since germinated. Clearly, the absence of the obligate pollinator was the only constraint to the establishment and spread of these species in southern Florida (McKey and Kaufmann 1991).

As with pollination, the degree of restriction to one or a few hosts and fungal mutualists varies widely. Some fungi appear capable of infecting many hosts or forming symbiotic relations with many hosts; some hosts appear able to form a mutualism with a wide array of fungi. Alternatively, some species are much more restricted; pines are perhaps the most well-known examples. The genus does not have native members in Australia, South America, or all but a northern strip in Africa (Critchfield and Little 1966), but all three continents contain climates that can support pines. Once soils on those continents were inoculated with appropriate mycorrhizal fungi, pine establishment was ensured. In fact, pines have become invasive locally on all three continents (Richardson et al. 2000, Richardson and Higgins 1998).

The spread of pines in the Southern Hemisphere is germane to the assessment of the causes of persistence because nonindigenous pines have rarely become established in the United States. Naturalized pines are largely restricted to *Pinus sylvestris* in New York State and *Pinus nigra* (Leege and Murphy 2001) on dune sets around Lake Michigan. The current restriction of pines is curious for at least four reasons. First, the conterminous United States has about 36 native pines that occur in a wide range of physical habitats (Critchfield and Little 1966), from some of the most arid habitats in which trees occur to sites with abundant moisture and from sites with air temperatures that routinely exceed 35°C to the upper timberline in the Appalachian, Cascade-Sierra Nevada, and Rocky Mountain ranges. Second, a long history of deliberate introduction of pines continues. *Pinus sylvestris, P. mugo,* and *P. nigra* are common horticultural species. Third, with so many native pines that all maintain associations with one or more native mycorrhizal fungi, it would be surprising if host extensions among the fungi to the introduced pines had not occurred. Finally, as with the inadvertent introduction of the requisite fungi in the Southern Hemisphere with potted pine seedlings from the native range, it would be surprising if similar introductions had not occurred in the long history of pine cultivation in the United States. The further naturalization and even invasion by foreign pines in the United States remain possibilities that should be experimentally evaluated.

LIFE HISTORY TRAITS

Thus far in this chapter, two major categories of factors that influence the process of establishment have been presented: stochasticity and environmental (abiotic and biotic) forces. However, no factor related to predicting the establishment of nonindigenous species has been pursued more assiduously or longer than a link between the life-history traits of species and their ability to become established in a new range. The reason is obvious: life-history traits are related directly to species growth, reproduction, and survival. The value of any such links is appealing and deserving of much further investigation. Having failed, however, to find broad taxonomic agreement between life-history traits and species' performance in new ranges, we outline here the traits that appear to play a role in influencing establishment for plants, pathogens, and insects.

Plants

Reproductive Systems

Although plants collectively display much diversity in reproductive systems, two fundamental dichotomies are apparent. First, reproduction can be sexual or asexual; and second, sexual reproduction can involve a single parent (uniparental) or two parents (biparental). Biparental sexual reproduction, often termed outcrossing, is the predominant form of reproduction in animals. It is also predominant among plants because of self-incompatibility mechanisms that promote crosses between individual genotypes and because of structural limitations, such as the separation of anther maturation and stigma receptivity in time (dichogamy) and space (herkogamy). Among dioecious species (in which separate plants are male or female) and those with self-incompatibility, pollen must be transferred from plant to plant if fertilization is to be achieved. Pollen flow might not occur in the absence of a suitable pollinator or if an individual is growing far from potential mates (Willson 1983). Dioecy does not, however, appear to be a major limitation for species establishment; there are dioecious invasive plant species, such as *Rumex acetosella, Ailanthus altissima*, and *Ilex aquifolium*.

Uniparental sexual reproduction arises from self-fertilization and is facilitated by hermaphrodite sex expression. As long as the flowers are self-compatible, plants with perfect flowers might have the ideal mating system for establishment in a new range. Species that usually display some form of uniparental reproduction also have an advantage as founders because the lack of recombination with other plants preserves multilocus genotypes related to increased fitness.

In contrast, monoecious species, which have separate male and female flowers on the same plant, might face the same limitation in pollination faced by dioecious species. Nevertheless, this limitation has clearly been overcome in some species, such as several pines (Richardson and Higgins 1998). Many perennial species that have been introduced into North America have the capacity for asexual reproduction by apomixis. Apomixis, which includes agamospermy and the clonal or vegetative regeneration of plant parts, allows isolated individuals to establish new populations and produce plants that are presumably adapted to the current environment. Agamospermy allows a plant to produce viable seed, often without the presence of any male gametes; this is an advantage of an isolated individual. In a comparative study of woody plant invaders and noninvaders, agamospermy was found to be slightly correlated with species that had become invasive (Reichard 2001).

Many plants have the ability to regenerate from a stem or root fragment or to resprout from a cut stem (Bell 1991). Vegetative reproduction of this type allows a population to increase rapidly and to regenerate quickly after a trauma. If the fragments are dispersed, as during a flood, distributed populations can be created. There are many examples of invaders for which most or all reproduction in the new range is the result of asexual reproduction. Clonal propagation is especially prevalent among invasive aquatic plants (reviewed in Barrett 1989, Barrett et al. 1993). In some cases, the failure to reproduce sexually occurs because of genetic sterility (as in *Salvinia molesta*) or the absence of mating types required for sexual reproduction (as in *Elodea canadensis*); alternatively, restrictions on sexual reproduction might arise because of unfavorable environmental conditions in the introduced range (as in *Eichhornia crassipes*).

The relation between reproductive systems and a population's ability to become established appears linked to the association between self-fertilization and colony establishment (Marshall and Brown 1981, Barrett 1982, Gray 1986, Brown and Burdon 1987). Single self-compatible individuals, with the capacity for autonomous self-pollination ("selfers"), are capable of forming established populations through self-fertilization, whereas self-incompatible or unisexual individuals require the simultaneous arrival of mating partners and pollen vectors (in animal-pollinated species) for reproduction. That simple idea, known as Baker's law (Baker 1955, Pannel and Barrett 1998), states that self-compatibility is favored among immigrants after long dispersal. It has also led to the prediction that annuals and nonindigenous ruderals (plants that commonly occupy rubbish piles and areas that are frequently disturbed), which depend on recurring dispersal and establishment, are more likely to be selfers than obligate outcrossers. Broad surveys generally support the association between self-fertilization and ruderals (Mulligan and Findlay 1970, Price and Jain 1981), although this pattern is less evident among perennial ruderals, many of which invest heavily in clonal offspring and are also outcrossing (Marshall and Brown 1981, Crawley 1987). Among flowering plants, increased longevity is generally associated with decreased selfing: annuals display the highest selfing rates, followed by herbaceous perennials. Woody perennials are predominantly outcrossing; few woody species are reported to have high levels of selfing (Barrett et al. 1996).

Surveys of plant invaders show that those which rely on sexual reproduction are not all selfers; this indicates that some outcrossers overcome this constraint during establishment. Pannel and Barrett (1998) evaluated the benefits of reproductive assurance in selfers compared with outcrossers in the context of colony formation in a metapopulation. Their results suggest that an optimal mating system for a sexual invader should include the ability to alter selfing rates according to local environmental and demographic conditions. When populations are small or individuals are at low density during the early phases of establishment in a new range, plants should be selfers to maximize fertility, thus increasing population growth rates. However, when populations become large and pollinators or mates are not limiting, outcrossing and its attendant genetic effects will be more beneficial.

Flowering and Fruiting Periods

A long flowering time ensures that a plant's flowers are receptive when pollinators are available. If a plant has a protracted season of flowering, the probability of fertilization is increased. Annual ruderals in Great Britain (Perrins et al. 1992a) and invasive woody plants in North America (Reichard 1994) have been shown to have a long flowering period. The latter study also showed that a long flowering time correlates highly with the length of the fruiting period. Similar to the case with the length of the flowering period, a long fruiting period can provide a greater opportunity for seed dispersal. So far, however, these traits have been of little use in predicting which species will be invaders across the broad taxonomic groups of potential immigrant species.

Juvenile Period

The juvenile period is the time from seed germination to the onset of flowering. A short juvenile period could allow a population to increase rapidly while decreasing the probability of the population's detection by predators, foragers, and pathogens before its sexual reproduction. Annual plant species, by definition, have a short juvenile period; ruderal or weedy annuals have a shorter juvenile period than nonweedy species (Perrins et al. 1992b), as do invasive woody perennials (Reichard 1994). Length of the juvenile period can be difficult to determine accurately for woody species, for which several years can elapse before onset of reproduction. Length of the juvenile period has been used repeatedly to predict persistence of nonindigenous species (Rejmanek and Richardson 1996, Reichard and Hamilton 1997, Pheloung et al. 1999).

Seed Production

Species with high seed production on an annual or cyclical basis are more likely to become established if their seeds are readily dispersed (Juenger and Bergelson 2000), because the odds are greater that some fraction of the seeds will reach sites suitable for germination. But incorporating this trait into any prediction of establishment is difficult because the level of seed production can be difficult to quantify for newly introduced species, especially woody plants.

Dormancy

Given the influence of environmental stochasticity on establishment, there should be strong selection for life-history traits that reduce its impact on a population. Seed banks buffer against the wide swings in the size of the vegetative population that result from strong year-to-year variation in resource availability (Cohen 1979, Venable and Lawlor 1980, Brown and Venable 1986, Phillipi 1993). Germination cuing, in which environmental signals correlated by habitat quality are sensed by seeds and trigger germination or induce dormancy, is a potentially important form of adaptive dormancy in plants. Given the potential for seed dormancy and germination cuing to reduce the demographic impacts of environmental stochasticity, it is not surprising that both dormancy and germination cuing are widespread in many agricultural (and predominantly nonindigenous) weeds (Cousens and Mortimer 1995).

Light Requirements

The ability to use light efficiently may enhance a plant's ability to live in areas with extensive canopies. Consequently, the ability to establish may be related to this trait. The extent to which shade tolerance is an attribute shared widely among naturalized plants is unknown but deserves systematic survey. Baruch et al. (2000) examined 10 physiological and morphological plant traits of four invasive members of the Melastomataceae (two herbs, a shrub, and a tree) in Hawaii and found that the invasive species were better suited to capturing and using light than a large group of natives.

Pathogens

Life-history traits important for the establishment of plant pathogens include reproductive strategies and genetic variability related to fitness, virulence, and host compatibility.

Reproductive Strategies

As with plants, pathogens use many reproductive strategies. Some pathogens (such as viruses and some fungi) reproduce only in the presence of their hosts, whereas others (for example, many fungi) are facultative saprophytes and do not require the plant host for reproduction. Some fungi reproduce only sexually, whereas many pathogens, such as viruses and some fungi, reproduce only asexually. Some pathogens can complete several generations in a single year, whereas others require several years to complete a single generation.

Asexually reproducing pathogens are thought to establish most easily (Agrios 1988). Another major characteristic of invasive pathogens is a high rate of survival when the plant host is not present (for example, in the winter for pathogens that infect the leaves of annual plants and deciduous perennials) or when the physical environment is totally unfavorable. Survival can occur in a dormant state (for example, in overwintering spores), in a saprophytic condition, or as infections in alternative hosts (Agrios 1988).

The most successful pathogens display a short time between one infection cycle and the next, have a high rate of production of infectious units (spores, bacterial cells, nematode cysts or eggs, or viruses), and have a long infectious period–the time that infectious units are produced or plants are contagious (Campbell and Madden 1990). Races of *Puccinia helianthi,* the sunflower rust pathogen, illustrate this point. The rust's superior colonizers have higher spore germinability, more rapid spore germination, more rapid formation of appressoria (spore-producing structures), and higher spore production than other genotypes or races (Prudhomme and Sackston 1990).

Genetic Variability in Fitness and Virulence

The characteristics described above might increase the potential for establishment, provided that the pathogens are carried to a genetically compatible host. Although it could be predicted that successfully established pathogen populations would have a wide range of virulence genes (Lawrence and Burdon 1989), this is not routinely the case, particularly in an agricultural context. Pathogen populations typically have the smallest number of virulence genes needed for survival, presumably because carrying unneeded virulence genes imposes a fitness penalty on the pathogen. Common, widespread pathotypes of *Pyricularia grisea,* the fungal cause of rice blast, always have fewer virulence genes than rare pathotypes–an observation that is consistent with the theory of a fitness disadvantage of accumulated virulence genes (Mekwatanakarn et al. 2000).

It is, however, the continuous generation of novel pathogenic variation that enables pathogen populations to overcome resistance and find susceptible hosts (Mekwatanakarn et al. 2000). A large local effect on the diversity of races and complexity of virulence occur in a pathogen population as it changes in response to host resistance (Andrivon and de Vallavielle-Pope 1995). The importance of variability in virulence for establishment tends to be greater among pathogen populations with narrow host ranges. High complexity for virulence is often found in clonally (asexually) reproducing pathogens, such as *Pyricularia grisea tritici,* that have long faced race-specific host-resistance genes (Marshall 1989; 1993). Conversely, populations of fungi with frequent sexual reproduction, such as the powdery mildews, often have fewer races but a greater diversity of virulence phenotypes (Roelfs and Groth 1980, Groth and Roelfs 1982).

Because of the local effect of selection by host resistance on the diversity and complexity of the pathogen population, immigrations by new genotypes are often detected on the basis of abrupt changes in pathogenicity or mating type. That was the case in Europe with *Phytophthora infestans,* the late blight disease pathogen (Fry et al. 1992). Some migrations are cryptic, especially if the virulence pattern of a pathogen population has not been monitored. However, information about the genetic diversity in pathogen populations can also help to reveal new introductions. For example, *Sphaeropsis sapinea* is an asexually reproducing fungus on Pinus spp. in South Africa, so it could be predicted that its population should consist of clonal lineages. But surveys revealed populations of high genetic diversity, a situation consistent with the occurrence of multiple introductions from different sources over a long period (Smith et al. 2000). Finally, in some wild host-pathogen combinations, extinction and recolonization occur routinely, and these outcomes suggest that migration and gene flow are important contributions to the genotype diversity of the pathogen (Burdon et al. 1995).

Rate of Population Growth

The net effect of whether a pathogen will come into contact with a susceptible host and the chance that such a contact will result in infection are summarized by the intrinsic rate of increase (r) or, more mechanistically, the basic reproduction number (R_0), sometimes called the progeny-parent ratio (Madden et al. 2000, Swinton and Gilligan 1996). A pathogen will be established only if R_0 is greater than a threshold, which is typically 1.0 (higher for small founder populations subject to the effects of stochasticity). An adequate way of determining a threshold of R_0 for persistence over more than one growing season, which incorporates survival and within-season dynamics, has not yet emerged, because of the difficulty of incorporating temporal discontinuities (periods without a susceptible crop) into the predictions (Gubins and Gilligan 1997, Madden and van den Bosch 2000).

Insects

Mating Systems

Insects and other arthropods usually arrive in a new range in small numbers and must reproduce and increase in density rapidly if they are to become established. Parthenogenesis and other forms of uniparental reproduction, such as mother-son or sibling mating, can facilitate survival of low-density populations or populations surviving in small refugia. Parthenogenesis results in a relatively high ratio of reproductive potential for each unit of resource, enabling nonindigenous organisms to exploit a resource rapidly when ephemerally favorable conditions arise (Niemelä and Mattson 1996). The search for mates can impede establishment if the loss of individuals dispersing to search for mates exceeds the rate of population growth (Lewis and Kareiva 1993). Parthenogenic forms of reproduction can reduce or even eliminate the need to locate mates.

Uniparental reproduction can facilitate the survival of a small population, but inbreeding depression can eventually become problematic in such populations, depending on the rate of mutation or the rate at which new, unrelated individuals join the population. However, populations of parthenogenic insects that are highly inbred might exhibit little inbreeding depression in fitness if most individuals with deleterious recessive alleles are lost. In addition, parthenogenesis is often linked with polyploidy and high heterozygosity, facilitated by apomixis. These traits presumably confer broad ecological tolerances for new and varying environments (Bullini and Nascetti 1990, Craig and Mopper 1993, Niemelä and Mattson 1996).

Parthenogenesis does appear to be frequently associated with establishment of nonindigenous insects. A large fraction of the nonindigenous invertebrates that became established in Hawaii are parthenogenic or hermaphroditic (Howarth

1985 cited in Simberloff 1989). In Europe, parthenogenic polyploid species of weevils have a much greater range than ancestral species that retain bisexual, diploid reproduction (Suomalainen et al. 1976), and several of these polyploid species have become established in North America. Parthenogenesis is more common among European than North American phytophagous insects and might partly explain the asymmetrical proportion of European invaders around the world. For example, roughly 40% of nonindigenous tree-feeding insects exhibit some form of parthenogenesis, compared with an estimated 11% of native tree-feeding insects in North America (Niemelä and Mattson 1996).

Several parthenogenic insect taxa have been particularly invasive in North America. At least 45 species of Coccoidea scales are established on North American woody plants (Mattson et al. 1994, Niemelä and Mattson 1996); these scale insects are characterized by several types of parthenogenesis and collectively display the most diverse chromosome system of any animal group (Kosztarab 1987). All 60 of the nonindigenous sawfly species and all 23 aphid species established on North American trees and shrubs are parthenogenic (Smith 1993, Niemelä and Mattson 1996). At least 65% of the 33 nonindigenous species of bark beetles (in the family Scolytidae) are facultatively parthenogenic (Atkinson et al. 1990). Establishment of parasitic hymenopterans introduced for biological control is probably favored by reduced inbreeding depression arising from haplodiploidy and the ability to adjust sex ratio according to population density, host condition, or other factors (Simberloff 1989).

Although parthenogenesis is associated with some insect invaders, this trait is not common to all invasive insect taxa. Niemelä and Mattson (1996) compiled data for eight dominant taxa of nonindigenous insect herbivores of woody plants established in North America. Two insect families—including leaf hoppers (Cicadellidae), plant bugs (Miridae), and one moth family (Tortricidae)—have no parthenogenic species. Thus, parthenogenesis or other forms of uniparental reproduction may contribute to the establishment of some taxa but not all.

Rate of Population Growth

The likelihood of establishment of nonindigenous insects has long been assumed to be related to the intrinsic rate of population growth, r. It has been argued that the relative amplitude (coefficient of variation) of a population's fluctuations is the most important variable affecting the average lifetime of that population (Leigh 1981) and that a high r can reduce the chance of extinction in a founding population (Lawton and Brown 1986). In a review of biological control projects Crawley (1986) found that arthropods with high fecundity, short generation time, or female-biased sex ratios were more likely to establish than comparable arthropods with lower population growth rates. Pimm (1989) noted that across animal taxa, r is inversely correlated with individual longevity. He found that the combination of small body and high r was advantageous for the establishment of a founder population except at very low population densities (such as six pairs or fewer), when long-lived species would be expected to have a lower extinction rate. In two other studies, insects with small bodies and high *r* were found to be more likely to establish than insects with large bodies (Crawley 1986, Lawton and Brown 1986).

Limitations in prediction arise, however, if estimates of *r* are used to predict the likelihood of establishment for a given arthropod species. One problem is that establishment can be linked to other life-history strategies. For example, in Crawley's (1986) review of biological control introductions, insects with long-lived adult stages were found more likely to establish. Adult longevity presumably enabled oviposition to occur over a protracted period, increasing the probability that the nonindigenous arthropod would encounter suitable conditions for establishment. In addition, *r* is often considered on a relative or qualitative basis, and it is not clear how large it would need to be to enhance the probability of establishment. Furthermore, it is difficult to disassociate *r* from other traits, such as reproduction strategy, dispersal, and interactions with predators or other taxa in a new habitat.

KEY FINDINGS

The numerous factors identified in this chapter form a basis for predicting the establishment of a nonindigenous plant or plant pest. The degree of uncertainty in our ability to measure these factors depends on whether the identity of the immigrant is known, whether important information about its life history is available, and whether the circumstances of its introduction have been accurately assessed.

Stochastic Forces

- The likelihood of establishment of nonindigenous plants and plant pests depends in part on the number of organisms that are introduced and the frequency of the introductions. Nonindigenous plants and plant pests typically arrive in small numbers and are vulnerable to demographic, environmental, and other stochastic forces that drive small populations to extinction.
- The chance of extinction due to demographic stochasticity is a function of the number of immigrants, their reproductive rate, and, if sexually reproducing, their success in finding mates. Populations of plants and arthropods of fewer than 50 individuals are highly vulnerable to extinction.
- Genetic bottlenecks, small size of the founder population, and strong directional selection on immigration can reduce the probability of establishment. Inbreeding in low-density populations can reduce the fitness of progeny. There are cases, however, where reduced heterozygosity resulting from a genetic bottleneck has enhanced the success of a nonindigenous species. Effects of such

genetic changes can profoundly alter behavior and social organization and alter ecological interactions between nonindigenous and native species.

- Environmental stochasticity can reduce populations to the level at which demographic stochasticity becomes important. Models derived for plants suggest that when deterministic growth rates of newly arrived species exceed 1.2, effects of environmental stochasticity will be reduced and extinction will occur only as a result of extreme environmental events.
- Weather, the random expression of the amplitude of climate, is an important source of adverse environmental stochasticity.
- Natural catastrophes—such as fires, floods, and earthquakes—are difficult to predict but can cause the extirpation of populations of less than several thousand individuals.
- An Allee effect arising from low reproductive success or survival in low-density populations can strongly influence the ability of a newly arrived, nonindigenous species to persist. Whether a founder population persists or is driven to extinction can depend on the strength of this inverse density dependence, the population process that is subject to the Allee effect, and interactions with environmental stochasticity.
- Phenotypic plasticity, including acclimation, may buffer populations from environmental stochasticity.
- Human-generated disturbance can reduce populations to the point where demographic stochasticity causes extinction. But cultivation, whether deliberate or inadvertent, can promote persistence of nonindigenous plant pests by increasing resource availability and decreasing environmental stochasticity.
- Spatial distribution of newly arrived populations can affect the influence of stochastic forces. Small populations that are restricted to a specific habitat or host are more susceptible to extinction from stochastic forces than populations distributed across a large geographic area or populations that occupy multiple habitats or infest several hosts.
- Demographic, environmental, and other stochastic forces can be overcome by repeated introductions of a species that increase its population number, by introductions that spatially distribute the population, and by the life-history traits (such as diapause and dormancy) that minimize the consequences of stochasticity.
- Estimates (based on interception or other data) of the size of an immigrant population, the frequency of introduction, and opportunities for it to be introduced in multiple locations could be useful in determining the likelihood that a nonindigenous population will become established.

Climate

- The geographic distribution and range of climates known to be suitable for the immigrant species in its native range or in previously invaded regions provide some indication of new habitats in which the immigrant population could persist. However, commodities that may harbor pests are often distributed from their initial entry point to other areas in the United States, which together encompass broad climatic variation (from arctic to generally tropical climates).

- Newly arrived organisms must be in seasonal synchrony with conditions in the new range. Nonindigenous organisms must enter and break diapause or dormancy at appropriate times. Among arthropod introductions in the Northern Hemisphere, species from northern latitudes that are introduced into southern latitudes may be more likely to become established than vice versa.

Host Plants

- Availability of suitable host plants is a critical factor in the establishment of nonindigenous arthropods and pathogens. Taxonomic similarity (at the genus or even family level) between host plants of insects or pathogens in the native and new ranges increases likelihood of establishment, although this relationship requires further testing.
- Broad diet breadth may enhance the likelihood of a phytophagous arthropod's establishment, especially if the flora in the new habitat is phylogenetically distant from flora in the native habitat. Most nonindigenous insects known to be established in North America, however, have specialized diets.
- Host plants must be temporally and spatially available to newly arriving nonindigenous insects and pathogens for their establishment in the new range.
- A vector is necessary for the establishment of some pathogens; in these cases, abundance, spatial distribution, and temporal availability of the vector will affect establishment.

Natural Enemies and Competitors

- The presence of competitors and natural enemies in the new range of a nonindigenous plant or plant pest may prevent its establishment. Effects of these biotic forces on new species are difficult to predict, however, and often require detailed ecological information that is rarely available.
- Immigrant arthropods or pathogens without a morphological counterpart or close familial relative among the native species could have an advantage in establishment if native natural enemies do not attack them.
- Native insect predators are more likely than native parasitoids to prevent establishment of new arrivals of herbivorous insects. Effects of entomopathogens on new arrivals of insects are largely unknown.
- There is little evidence that competition with native species has prevented establishment of new arrivals of insects or pathogens, although this could theoretically occur.
- Competition, especially for light, can substantially affect the establishment of nonindigenous plants.

Species Traits

- Selected life-history traits are frequently associated with persistent nonindigenous species and may be useful in predicting or assessing the likelihood of establishment of a given species. However, many exceptions occur for any given trait, and most can be evaluated only subjectively or qualitatively. Quantitative comparisons between the traits of species that have become established and the traits of species that have failed to establish are rare, especially for arthropods and pathogens. Nevertheless, there are traits that appear to enhance establishment, and these require much further study.
- The ability to change from outcrossing to selfing in response to local environmental conditions could optimize the opportunity for establishment. Species with high phenotypic plasticity among many ecologically important traits (for example, the traits collectively considered in connection with phenology) also have an advantage in a new environment. Possession of a resistant dormant phase, particularly a resistant seed bank, appears important, as do alternative forms of asexual and sexual reproduction, rapid growth, and high fecundity.
- Nonindigenous plant pathogens with genetic variability in traits associated with reproduction have a higher probability of establishment. Traits of plant pathogens that appear to enhance establishment include a short infection cycle, high productivity of infectious units, and a long infectious period.
- High intrinsic rate of increase, uniparental reproduction, and a dormant or resilient life stage that permits surviving temporally unfavorable conditions characterize many insect invaders. Other life-history strategies, such as long-lived adult stages, are common among established nonindigenous insects.

4

Biotic Invasion

Few events are as important in predicting the future role of a nonindigenous plant, arthropod, or pathogen as its attainment of the population size at which it rapidly adds members and spreads simultaneously into a new range (Elton 1958). In this demographic and geographic transition, the species is no longer likely to go extinct through stochastic forces—losses to environmental stochasticity are all within limits that can be absorbed by the population. The population's basic reproduction number (R_o) is greater than 1, and its deterministic growth rate (λ) will be increasing from 1; hence, the population doubling time will be decreasing. The population is not simply tolerating its new range; the environment of the new range is clearly well within the species' ecological amplitude. Furthermore, the totality of its traits contributes to its survival in the new range and to its proliferation. In the terms used in this report, the species has become a biotic invader.

An issue in this report is why some species make a transition from low to high rates of population growth, that is, shift from being simply persistent or surviving to becoming invasive. An explicit explanation is needed, one ideally based on the attributes of the species combined with its circumstances in the new range. From the case histories of individual invasions, it is apparent that the transition in each case has been propelled by a unique and accidental chain of events in which community dynamics and the resources of the environment interact with the biological characteristics of an established species in a way that fosters its proliferation (Crawley 1989a). At each turn, these events enable other traits to reinforce the growth and spread of the population. The nexus of the community, its environment, and the size of the population is crucial, but so little is known quantitatively about many of these interactions that using them in a predictive manner remains difficult.

Among the factors that influence an immigrant's transition from persistence to invasion are the same abiotic and biotic forces that are faced by organisms during establishment. For example, the establishment of nonindigenous arthropods has often been attributed to their escape from natural enemies in their native habitat. However, knowing whether resident enemies in a newly colonized habitat will attack a nonindigenous arthropod and limit its demographic growth or spread is important if we wish to predict which immigrants will not only establish, but also proliferate and spread.

Cornell and Hawkins (1995) and Hawkins et al. (1997) compiled life tables for herbivorous insects and examined patterns in mortality caused by natural enemies to determine whether established nonindigenous species sustained lower mortality from resident natural enemies than did natives. In the first report, Cornell and Hawkins (1995) found that the invasion status of the herbivores was only weakly related to the mortality caused by natural enemies. Sources of mortality differed most strongly between early-stage and late-stage herbivore larvae and between insects that feed inside plants (endophytic) and insects that feed externally (exophytic). Hawkins et al. (1997) used slightly different methods to differentiate among causes of mortality in 63 resident and 20 invading species. Nonindigenous insects did not sustain lower overall mortality than natives from resident natural enemies, but larvae and pupae of nonindigenous species experienced more predation mortality and perhaps more pathogen mortality than natives, although differences were not statistically significant. It must be noted, however, that the analysis relied on data collected in life-table studies of economically important insect species; this suggests that the nonindigenous species included in the analysis had successfully made the transition from establishment to proliferation and spread. Knowing whether interactions between nonindigenous insects and native natural enemies are similar earlier in the invasion process will require additional research.

Evidence from existing studies, however, could be useful in developing testable predictions about the effects of native natural enemies on nonindigenous insects that have become established in the United States. For example, we might expect that nonindigenous insects that feed externally on plant foliage, where they are exposed, will be more likely to acquire a complement of native predators than insects with more protected or specialized feeding behaviors. We might also predict that native parasitoids that are habitat-specific, rather than host-specific, could eventually become an important cause of mortality among nonindigenous insects, especially those confined within leaf or phloem tissue. In a review of cases involving insects imported for weed control, endophytic herbivores were the group most likely to experience mortality from native parasitoids (Goeden and Louda 1976). Native endophytic leaf-miners sustained the highest mortality from parasitoids in the analysis by Hawkins et al. (1997). Bright (1996) noted that the ability of native parasitoids to successfully attack larvae of the larger European pine shoot borer (*Tomicus piniperda L.*) in pine logs was not surprising, given that the parasitoids are habitat-specific rather than host-specific. Furthermore, Hawkins and Gross (1992) showed that parasitoids reduced the density of nonindigenous herbivorous insects more often if the native habitat of the herbivores supported many parasitoid species than if it supported few such species. Thus, information about the diversity, life history, and importance of natural enemies in the native habitat will be valuable in estimating the potential effects of the resident enemies on the dynamics of newly established nonindigenous insects.

The longer a population is established and is expanding into a new range, the more likely it is to come into contact with a greater diversity of conditions and organisms (Strong et al. 1984). Over the longer term, in addition to the factors discussed in Chapter 3, a species' invasion will be influenced by factors that may have been less prominent during establishment. This chapter discusses three processes that occur in an invasion: dispersal and spread, competition for resources, and evolution. The few elements of these processes that we know about offer clues to predicting invasiveness, but this information is incomplete, and the gaps in our knowledge suggest potentially productive lines of research.

DISPERSAL AND SPREAD

Once an immigrant population has arrived, it will become a successful invader only if the population is able to increase in abundance and spread from its point of entry. Spread of a nonindigenous species in a new range is determined by several components, including the number of propagules available for dispersal, the opportunities for and mechanisms of dispersal, the communities into which the organism spreads, and the availability of suitable hosts, nutrients, and other resources in the habitat. The difficulty of predicting the rate of population growth and spread is often compounded by interactions between life-history traits of the organism and characteristics of the environment.

Expansion of an immigrant population consists of three steps: an initial establishment phase with little or no expansion, an expansion phase, and a saturation phase (Shigesada and Kawasaki 1997). Shigesada and Kawasaki (1997) describe three situations that can initiate the beginning of the expansion phase. In some species, expansion begins only after the territory occupied by the initial invading population becomes filled. When the population is subject to an Allee effect, the time for the initial population density to reach this level will be increased (Lewis and Kareiva 1993). In other species, expansion begins only after the occurrence of a favorable mutation in the colonizing population. In other words, expansion is triggered by a genetic adjustment to the new habitat that leads to higher fecundity, survival, improved dispersal ability, or some other significant trait (Bazzaz 1986). In the third scenario, a few individuals that were initially released into a single area disperse rapidly. Range expansion becomes evident only when reproduction enables these populations to increase above a detection threshold.

The rate at which expansion proceeds can be assessed by evaluating the relationship between range distance and time. According to Shigesada and Kawasaki (1997), the shape of the curve relating range distance and time can assume three general forms. The range of a population with a type 1 curve expands linearly with time. Offspring typically settle in the neighborhood of the parent population, and dispersal occurs primarily over short distances. Shigesada and Kawasaki (1997) suggest that natural expansion of gypsy moth populations, which occurs when recently hatched larvae balloon on the wind, may exemplify a type 1 curve.

In contrast, species with a type 2 or type 3 curve are able to expand their range not only by random movement into surrounding adjacent areas, but also by long-distance dispersal, a process referred to as stratified diffusion (Andow et al. 1993, Hengeveld 1989). These populations will demonstrate an accelerating range-versus-time curve. A population with a type 2 curve initially expands slowly, then linearly at a higher rate. Short-distance migration expands the occupied area from its periphery; long-distance migrants generate new satellite colonies that expand in isolation for a short period until they coalesce with the parent population. In a population with a type 3 curve, the rate of spread increases linearly with time, and the curve assumes a convex shape. In this scenario, long-distance migrants establish satellite colonies; in the long run, the range of these colonies expands independently of the parent population and other colonies. Hengeveld (1989), however, noted that an accelerating range-versus-time curve could also reflect genetic adjustments early in the expansion phase.

In some plant-pathogen populations, movement of propagules away from the source population follows a dispersal gradient that reflects the population's net reproductive rate and the dispersal distances of the propagules. When spores settle rapidly from the air, the distribution of propagules will be exponential and the expansion rate will be roughly linear with time. In such a population, the radius of the focus increases linearly with time (Shigesada and Kawasaki 1997, van den Bosch et al. 1990), and new foci developing ahead of the wave front will be subsumed by the front (for example, a type 1 curve). However, if the distribution of propagules is not exponentially bounded, propagules are disseminated further from the focus. If new foci are not subsumed within the much larger foci of the invasion, the average population expansion rate increases with distance from the original focus (Shaw 1995). Growing evidence indicates that the latter type of distribution occurs commonly in many plant-pathogen species (Ferrandino 1993), and this type of distribution apparently operates among different taxonomic groups. Establishment of multiple foci accelerates the spread of a population. Moody and Mack (1988) showed that spatially growing foci expanded in area as a strict function of their circumference-to-diameter ratio. Thus an area could be occupied by an invading species much sooner if the species is distributed as an array of widely separated foci than if the composite area occupied by foci is expanding from a much larger, single focus, unless they are expanding at a markedly lower rate (Moody and Mack 1988).

The relationship between the number of foci and the dispersal distribution provides one explanation of the change in the rate of expansion of a nonindigenous species from the so-called lag phase to the log phase. Initially, the immigrants and their immediate descendants are confined to a small area, a "beachhead" that consists of a single focus in the new range. Propagules of this population may be carried well beyond the beachhead, and some fraction is able to establish new foci. These foci are a threshold or minimum that precipitate the log phase of range expansion; they are both expanding and creating new foci, and range expansion accelerates markedly. The emergence of the pronounced range expansion depends, of course, on multiple demographic and biotic factors (such as competition, predation, parasitism, and resources), not the least of which is sufficient distance between nascent foci for them to add individuals to the unoccupied range. Convergence among foci would create the potential for intraspecific competition, which could partly explain why a population expanding spatially from a single large focus occupies space so much more slowly; many offspring land in an area that is already occupied, as opposed to being carried far from the population boundary. The transition from a species that is persistent or merely surviving in a new range to an invasive species might simply represent the time and opportunity for a nonindigenous species to be transported to some minimal number of isolated locales where new foci establish and expand. The minimum is probably unique to each species and perhaps even to each combination of locales at which a given species arrives.

Life history, morphology, and behavioral traits related to dispersal of a newly established species obviously play important roles in determining the rate of range expansion (Hastings 1996), and knowledge of such characteristics would be useful in predicting the likelihood of invasion. The process of dispersal facilitates cued responses to environmental variables or "bet-hedging" by species in unpredictable or harsh environments (Levin 1989). Dispersal can reduce dependence of populations on localized climatic variables, enabling the presence or abundance of an invader at a specific location to be influenced by spatially disparate populations (Davis et al. 1998). Source-sink dynamics enable invader populations to be sustained in less than optimal conditions through frequent or continued immigrant dispersal from source populations (Davis et al. 1998, Pulliam 1998). Emigration and immigration among colonies can counteract environmental stochasticity, however, only if the individual colonies are exposed to independent environmental events and if they are close enough for dispersal to occur (Lewis and Kareiva 1993, Stacy and Taper 1992).

Populations of numerous plants, insects and plant pathogens include forms or behaviors that lead to both short- and long-distance dispersal, consistent with the type 2 or 3 curves described by Shigesada and Kawasaki (1997). In some moth and locust species, for example, long-distance dispersers become more common as population density increases. Long-distance dispersal can also occur when plants' propagules are carried by insects, wind, or water or by birds or mammals. In addition, our ability to detect a newly established population is typically limited when the density of a population is very low. The population must exceed a threshold density before it can be detected; this threshold will depend on traits or behavior of the organism, including the extent of the damage it causes.

Dispersal information about a species is often anecdotal and usually lacks quantification (Ridley 1930). Comparisons of biotic and abiotic dispersal among woody invaders and noninvaders suggested that the dispersal mechanisms of a species were not predictive of its likelihood of becoming invasive (Reichard and Hamilton 1997). Data from mark-recapture studies of 12 plant-feeding insects indicated that variation in diffusion was considerable among ecologically similar species and even within the same species (Kareiva 1983). In addition, inadvertent transportation of a nonindigenous organism by humans can establish new foci at substantially greater distances than would occur by natural dispersal mechanisms of the species. Such transportation has been shown to have substantially increased the spread rate of such species as gypsy moth (Liebhold et al. 1992) and cereal leaf beetle (Andow et al. 1993). Differences in dispersal, however, have been recognized among plant community types. Wind dispersal, for example, is more common among arid treeless ecosystems, and bird dispersal is more common in forest systems. Special attention should be given to the detection of newly established species with large, fleshy fruits in habitats that support an array of frugivorous birds. Such birds have contributed substantially to the spread of naturalized species, such as *Clidemia hirta* (Koster's curse) and *Hedychium gardnerianum* (kahili ginger), in Hawaii (Cuddihy and Stone 1990).

The economic and ecological importance of invasive species has given rise to numerous models that seek to describe how invading species spread and increase in abundance (Liebhold et al. 1992). In a simple diffusion model, the range of an immigrant expands solely by diffusion without population growth. In other words, the population expands in a concentric manner around the origin, and the density of the population decreases rapidly away from the origin.

Logistic expansion occurs when a population spreads by growth alone without diffusion (Skellam 1951). In that case, the rate of spread will depend on the reproductive rate of the organism and the degree of competition it encounters. If competition does not occur, the relationship between rate, distance, and time approaches a Malthusian curve. When competition increases with density, however, a logistic curve results because growth slows as population density increases. The spread rate becomes asymptotic as the population approaches the carrying capacity of the habitat.

Perhaps the most widely used model to describe the spread of an invader is a growth-diffusion model that links an exponential population growth term with a diffusion model (Fisher 1937, Liebhold et al. 1992, Skellam 1951). Range expands because of the combined effects of diffusion and growth, and the change in population density over time is approximated by an asymptotic rate of spread. The advancing front of the population will appear to advance at a constant velocity and shape–a wave front. As described by Shigesada and Kawasaki (1997), such a scenario occurs when the density of the initial colonists invading the origin decreases rapidly because of diffusion and there is little competition. As the population gradually recovers through reproduction, competition effects start to be manifested, so the density in the occupied range approaches the carrying capacity of the habitat. The range front forms a sigmoidal pattern and spreads at a constant speed–a traveling frontal wave. At the edge of the expanding population, competition is low, so expansion by diffusion predominates and density-dependent effects on growth rate are insignificant. Despite its relative simplicity, the growth-diffusion model has been used successfully to simulate the spread of a variety of organisms (Hastings 1996, Levin 1989, Liebhold et al. 1992, Long 1977, Willamson and Brown 1986).

More-sophisticated models with additional variables may be needed when an organism is transported by wind or water or tends to orient to a stimulus. For example, in a convection model, a velocity term is applied to the reaction-diffusion equation, which may better describe an insect, plant, or plant-pathogen species that is transported by wind (Lewis and Kareiva 1993). Insects may select their flight direction or respond to host or conspecific volatiles, whereas the spread of seed or pollen may be affected such variables as settling velocity, height of release, wind speed, and turbulence (Okubo and Levin 1989). Spread of populations can be linear or streamlike if dispersing propagules are channeled by topographic or climatic factors (Carey 1996).

If the population is influenced by an Allee effect, success or failure of an invasion may be determined before the asymptotic form of expansion is achieved (Lewis and Kareiva 1993). Presence of an Allee effect or an increase in the diffusion coefficient will require the initial "beachhead" to be larger if the population is to avoid extinction. Even if an immigrant population initially arrives in a new area at a density above its critical Allee effect threshold, an Allee effect will increase the period before expansion begins (Veit and Lewis 1996) and can substantially reduce the traveling-wave speed, resulting in a lower asymptotic rate of spread. Presence of an Allee effect will affect the curvature of the boundary between invaded and uninvaded regions and affect the rate of spread. When "fingers" of an uninvaded area protrude into the invaded area, the population will spread faster than when occupied territory curves sharply into unoccupied territory (Lewis and Kareiva 1993).

Environmental heterogeneity—for example, the patchiness of the environment—can also influence the rate of spread. Diffusion coefficients may vary widely, depending on the degree of environmental, habitat, or resource heterogeneity and how the nonindigenous species responds to the heterogeneity. When the habitat is not uniform, the expansion rate of a population will be affected by the spatial distribution of favorable and unfavorable patches (Shigesada and Kawasaki 1997). Environmental variables interact with biological traits of an organism, and this increases the difficulty of predicting invasion rates. For example, the spread of Scotch broom (*Cytisus scoparius*) from multiple foci was lower in urban areas than in prairies, primarily because survival and reproductive rates were lower in the less favorable urban habitat (Parker 2000).

Predicting the potential of populations of nonindigenous plants and plant pests to grow and spread will depend in part on what can be determined about the dispersal mechanisms and circumstances of organisms in any range, whether native or new. Studies are needed to quantify the role of the various factors—such as wind, birds, natural migrations, and human-mediated actions—that contribute to long-distance transport of individual species. Continued research into and documentation of the spatial and temporal aspects of known invasions will be necessary if we are to improve our understanding of patterns of range expansion and of the mechanisms by which invasions progress.

COMPETITION FOR RESOURCES

Community Diversity and Resources

Community diversity is viewed as the factor that most influences a community's susceptibility to invasion by nonindigenous species. Different theories (but few experimental studies) support opposing views of the role of diversity in invasion (Levine and D'Antonio 1999, Dukes 2001, Naeem et al. 2000, Stohlgren et al. 1999). Levine and D'Antonio (1999) argue that natural plant communities with high biodiversity tend to be more prone to invasion than their species-poor counterparts because the factors that control native diversity also control diversity among invaders. A supplemental argument is that the "microheterogeneity" of diverse communities provides differences in the spatial context (such as canopy height and rooting depth) that in turn provide more opportunities for immigrant species than are found in monocultures.

Those arguments are in contrast with the concept of "limited resources space", which suggests that the more species that occupy an area, the more fully resources are used and the more difficult it is for a new species to become established (Tilman 1987, 1988 and references therein, Knops et al. 1999). In addition, there are many cases in which nonindigenous species have become established in species-poor communities.

Indirect interactions among species can also facilitate invasiveness, regardless of diversity. Some species in a community can deter invasion; others can facilitate it (Palmer and Maurer 1997). Interspecific competition initially appeared to be responsible for the declining numbers of a native leafhopper after establishment by a nonindigenous leafhopper (Settle and Wilson 1990). Field and caging experiments showed that neither species was competitively superior; mortality caused by interspecific competition was equal to mortality caused by intraspecific competition. The two species did, however, share a parasitoid enemy, and the native leafhopper experienced higher attack rates by this parasitoid than did the nonindigenous leafhopper. Differential parasitism apparently shifted the competitive balance so that the native species was at a disadvantage compared with the nonindigenous species. Other studies have similarly shown that the establishment of a nonindigenous insect can be affected by complex interactions involving both potential competitors and resident natural enemies (Davis et al. 1998, Muller and Godfray 1997). Discussions about diversity and competition within communities often refer to the likelihood of invasion as depending on the availability of "vacant niches" for colonization. Observations that some island communities with simplified structures or impoverished floras are particularly susceptible to invasion have been used to support the possibility that they contain vacant niches (Elton 1958). As noted in Chapter 3, other explanations are possible, including the greater numbers of mainland species and the greater opportunities for them to be introduced to islands (Simberloff 1995).

The niche concept in general and the vacant-niche idea in particular are based largely on classical ecological theory that emphasizes the importance of interspecific competition in structuring communities. The validity of the niche concept in explaining community structure has been questioned, in part because the paradigm of competition as the primary organizing force in communities has been challenged (Simberloff, Connor, Strong, Wiens, etc). Crawley (1987) suggests that the confirmation that a niche is vacant is difficult without knowledge of the other factors that can render those resources unexploitable.

It would be more fruitful to focus on resource availability and how variation in limiting resources may foster or hinder the invasion process (Davis et al. 2000). Invasions of communities probably include both cases in which resources are usurped by an invader at the expense of natives and cases in which unused or underused resources are commandeered. *Centaurea solstitialis* (yellowstar thistle), for example, is able thrive with minimal water in the annual grasslands in California's Central Valley (Gerlach et al. 1998). Invasive nitrogen-fixing species have proliferated in habitats where there apparently were few native nitrogen-fixers or where native nitrogen-fixers operated weakly (Vitousek and Walker 1989).

A potentially productive approach to predicting invaders is examination of the functional groups in communities, regardless of the taxonomic groups involved. Community ecologists have long noted that some species appear to play similar roles in a community, for example, tree species that occupy different levels in the forest canopy at maturity, and diverse cryptogams that collectively form a crust-like layer in grasslands that are dominated by perennial grasses (Evans and Johansen 1999). They have also noted that some communities lack occupants in apparent roles. In New Zealand, for example, some of the *Nothofagus* forests in mesic environments have extraordinarily low species richness (Wiser et al. 1998); the forest understory can consist of fewer than 12 species. It is unlikely that the native resident species collectively play all the roles (and to the same degree) of light and nutrient capture as are played by the scores of species in Northern Hemisphere forests in similar physical environments. The testable question that emerges is whether the low species richness of the native New Zealand forests has led to their being invaded more than, for example, forests with similar physical environments in North America or Europe. The many examples of nonindigenous species that have become invasive with little or no continued assistance by humans suggest that such opportunities do exist.

Disturbance and Resources

Disturbance can alter the availability and use of resources. In general, ecological communities modified by human or exogenous natural events, such as hurricanes and cyclones, to a condition that is not otherwise common are considered more susceptible to invasion. The almost ubiquitous occurrence of ruderal (usually nonindigenous) species along roadways, footpaths, and pastures—sites of routine disturbance—is forceful testimony to this principle. In addition, disturbances that remove biomass and recycle limited resources create opportunities for colonization and occupancy by nonindigenous species, such as ragwort *Senecio jacobaea* (McEvoy et al. 1993, McEvoy and Coombs 1999) in Oregon. So strong is the link between disturbance and the proliferation of agricultural invaders that it becomes necessary to separate these cases categorically from those in which disturbance is minor or even nil. The degree to which plant invasions in natural communities have been not only sparked but also sustained by continual disturbance deserves further investigation (Mack 1989).

Competitive Traits and Resources

Once established, some invaders can usurp resources in a new range, use them more efficiently than the natives, or even alter the resources themselves. In many invasive species, these competitive traits are revealed as the organism begins to proliferate. Evidence of interspecific competition among newly established insects or pathogens is scarce, but competition often plays a substantial role in plant invasions. In many plant communities, competition for light is so intense that a nonindigenous species' ability to invade could be related directly to its ability to capture light that could otherwise be used by native species. So the "upmanship" or growth in stature that has arisen through natural selection since plants emerged on land is illustrated in some plant invasions. In its simplest terms, nonindigenous plants that can overtop their neighbors can replace them in the canopy, especially if they reduce light below the light-compensation point for any stage in the natives' life cycle. In some cases, climbing nonindigenous vines have reached the top level of the native tree canopy and altered light to the detriment of all species below them. Their influence, although often limited to the edge of the forest, can nevertheless severely affect species diversity locally. A classic example in the United States is *Pueraria lobata* (kudzu), but it is not unique, and apparently other naturalized climbing species are becoming invasive, such as *Paederia foetida* (skunk vine) in Florida (Schmitz et al. 1997) and *Bryonia alba* in the Pacific Northwest (Novak and Mack 1995). Thus, any nonindigenous species that can form a denser shade in a community than is formed under the native species could potentially become invasive. Competition for light is so intense among many plants in a wide array of community types in the United States (such as most forests, most perennial grasslands, and many wetlands communities) that special attention should be paid to the light-sequestering ability of any plant immigrants.

Some invasive plants have better-developed root systems (denser, more finely divided, or deeper) or more-efficient root systems than do natives. *Tamarix ramossisima,* which has a high rate of transpiration, has roots that extend far into the soil profile. This species' roots withdraw water from lower levels than do the roots of the native species (Horton et al. 2001a,b). Nonindigenous plants that produce more-abundant nectar or have more-abundant fruit than native species outcompete natives for visits from pollinators, and this results in reduced seed production among the natives (Sallabanks 1993, Brown and Mitchell 2001).

In addition to vying for resources that native plants require, invasive plants can alter the environment. The introduction of salt on the soil surface in the case of *Tamarix* or of nitrogen in the soil in the case of root-modulating plants can alter species composition and even succession (Vitousek 1986). An increase in the production of combustible fuel is perhaps the best-known environmental alteration caused by some invasive species. Some nonindigenous plants facilitate fire or alter the frequency or intensity of fires, whether by rapidly increasing fuel load or through the plant's chemical composition. For instance, in California chaparral, introduced grasses have increased the fire frequency markedly; this prevented native grasses from maintaining a sufficiently large seed bank and led to a reduction in the native grasses (Zedler et al. 1983, Jackson and Roy 1989). Attention in the United States has centered on *Bromus tectorum*, a long-term invader in the intermountain West that has devastatingly altered the fire regime and in turn the composition of plant communities in a vast area. The steppe communities in which *B. tectorum* is dominant have always burned, but the invasion of *B. tectorum* has increased the frequency of fire and probably its severity. The result has been major and probably permanent alteration of the species composition in these communities (Daubenmire 1970). High concentrations of resins and other highly combustible compounds and litter in far greater quantities than is cast by natives in a community are not in themselves characteristics of invasive species. But the entry of species with those traits or abilities should be a source of concern. If for unrelated reasons these species became invasive, they would alter the environment substantially (D'Antonio and Vitousek 1992).

Invasive species can also alter ecosystems through sediment deposition when they grow in areas of water flow where plants have not been found historically. Such alteration has occurred in the Bristol Channel in Great Britain. *Spartina anglica*, the invasive product of hybridization between North American and European species and subsequent chromosome doubling, is causing accretion of soil in the natural mudflat at rates of 8-10 cm/year (Ranwell 1964).

EVOLUTION

Genetic diversity can be important to a species' invasion in a new range. Much information has accumulated on patterns of genetic diversity among plant invaders in recent years, allowing some generalizations to be made. The two most obvious are that the genetic consequences of invasion vary widely among taxonomic groups, depending on their reproductive systems and life histories, and that many nonindigenous species have produced invasions despite their low genetic diversity.

As discussed in Chapter 3, many plant invaders have low diversity at marker loci, such as allozymes (reviewed in Barrett and Shore 1989), but this lack of diversity does not necessarily indicate that they lack genetic variation at all loci, particularly those governing quantitative traits related to fitness (Lewontin 1984, Brown and Burdon 1987). Population differentiation within an invading population after range expansion should be expected, even in species with relatively low variation at neutral marker loci. Studies of genetic differentiation in agricultural weeds or ruderals have often revealed evidence of race formation despite allozyme uniformity (reviewed in Barrett 1988, Warwick 1990). Mutation causes that discrepancy. Genetic variation in polygenic life-history traits is maintained, even in selfing populations, because polygenic mutation rates are considerably higher than those for loci coding for single proteins (Lande 1977). The tempo of differentiation varies considerably among species, depending on the balance between sexual and asexual reproduction and on life-history characteristics.

A source of variation that can favor the evolutionary diversification of invading species is the mixing of genes from multiple founders (Novak and Mack 1995). If there are introductions of a species from different portions of its native range, these will inevitably be genetically differentiated from one another because geographic variation is nearly universal. During range expansion, genotypes derived from separate introductions can cross with one another and give rise to highly variable offspring in the second and later generations. Many of the products of such crosses are likely to be maladapted to local conditions because of outbreeding depression (Templeton 1986), but through selection some individuals with appropriate gene combinations probably will arise from these "genetic soups". In that way, novel phenotypes that are locally adapted to conditions in

BOX 4-1 Sleeper Species

Sleeper species are those whose populations appear to remain in a quiescent phase for long periods before they begin to proliferate (Groves 1999). The current range expansion and proliferation of rocket (*Hesperis matronalis)* might qualify it for inclusion in this category. It was introduced early in the 19th century in the United States. It apparently became naturalized soon after arrival, but its numbers did not increase noticeably. In the last 10 years in eastern Washington, what had once been small isolated populations of the species are clearly becoming more abundant, and the individual populations are growing. It is premature to declare this once-inconspicuous species (R.N. Mack, personal observation) an invader, but its range expansion and increase in abundance could well lead to its playing that role.

The causes of the emergence of such nonindigenous species into a more prominent role may be related to intrinsic biological attributes or happenstance (Crawley 1989). Such cases could represent the emergence of a new array of genotypes in the nonindigenous populations through postimmigration selection; this proposal is attractive, but evidence among higher plants and animals has been elusive. The proliferation of sleeper species could simply represent the end of a protracted lag phase in the new range–a phase that has no definable limits. For example, *Opuntia aurantiaca* resided in low numbers in South Africa for over 80 years before it rapidly rose in prominence and abundance (Moran and Zimmerman 1991). Whether the increase was due to the emergence of new genotypes or to the attainment of the threshold number of foci for range expansion, or both, is unknown. Such range expansions would be more apparent if tied to a rapid and potentially radical change in the environment, particularly one fostered by disturbance. Probably many species have undergone such range expansion as some aspect of the new range environment was altered and the change favored their proliferation.

In contrast, the appearance of sleeper species can reflect our inability to detect new or recently established populations until some chance event occurs. Populations of Asian long-horned beetle and pine shoot beetle, for example, were established for at least 5 or 10 years before they were detected. They came to the attention of entomologists and regulatory officials once specimens were sent to an appropriate expert, but not necessarily because of increased population density or spread. In such situations, the points of entry and establishment and the initial rate of spread by founding populations can be difficult to identify; these limitations increase the difficulty of developing predictions.

Finally, when a nonindigenous species is mistaken for a congener, its spread goes unnoticed. In a park in Halifax, Nova Scotia, the brown spruce long-horned beetle (*Tetropium fuscum*) was collected in low numbers as early as 1990, but it was thought to be a closely related native species, *T. cinnamopterum*. It was not recognized as an interloper until numerous trees were dying in 2000, at which point beetles were collected from at least 23 other locations in the Halifax area and correctly identified. Such situations can be especially problematic when they involve groups of arthropods or plant pathogens whose systematics are not well understood.

the new range can potentially evolve. This scenario seems likely in the history of the plant invaders *Echium plantagineum* (Patterson's curse) in Australia and *Lythrum salicaria* (purple loosestrife) in North America; in both cases, there is evidence that multiple introductions from Europe resulted in considerable genetic diversity in introduced populations (Thomson et al. 1987, Burdon and Brown 1986). Such diversity is likely to favor rapid evolution of local races, despite recent efforts at biological control.

The idea that the mixing of distinct genetic lineages through multiple introductions can give rise to novel phenotypes is supported by evidence from hybridization studies in several flowering plant groups. For example, morphological and genetic evidence demonstrates that the recently derived allotetraploid ruderals *Tragopogon mirus* and *T. miscellus* originated in the U.S. Pacific Northwest through hybridization between allopatric species from Europe that were introduced in historical times (reviewed in Novak et al. 1991). Similarly, molecular evidence indicates that the common cattail *Typha glauca*, an important component of wetlands surrounding the Great Lakes, is a stabilized F_1 hybrid between the native *T. latifolia* and introduced European *T. angustifolia* (Kuehn et al. 1999). Not all hybridization events result in the origin of stable F_1 hybrids. Recent molecular studies of putative hybrids between the native Californian cord grass (*Spartina foliosa*) and *S. alternifolia*, an introduced species from the East Coast of North America, demonstrated extensive introgression between the two parental species in the San Francisco Bay (Ayres et al. 1999). Abbot (1992) discusses other examples of new plant invaders that arose from hybridization. Rhymer and Simberloff (1996) review cases in which such hybridization and introgression of plants and animals pose ecological and genetic threats to the survival of native species.

The capacity of nonindigenous species to evolve after their arrival in a new range complicates our ability to predict their postarrival behavior. Novel genotypes emerge through strong selection, hybridization, and the sharing of genes among members of the same species drawn from different parts of the native range. Selection in the new range sorts among these new genetic products, and the result can be organisms more adapted than their ancestors to the new range. As cited above, there are cases in the United States of new species, created through allotetraploidy, whose existence, to say nothing about their role in the new range, could not have been predicted. Those results have implications for current quarantine practices. With few exceptions, nonindigenous species already found in the United States are not barred from further entry. That practice has the unintended result of potentially allowing the introduction of a species' genotypes that were previously unrepresented in the United States. As has already occurred repeatedly, the continuous potential exists for the eventual assembly of new, invasive genotypes from among an array of genotypes each of which by itself is innocuous or at least only has the ability to become naturalized, not invasive. The degree to which this phenomenon has occurred and can occur, particularly among species with broad native ranges, should be the subject of active research.

Hybridization of related plant species originating in different areas can influence gene flow in their pathogens. That can have substantial evolutionary consequences, such as influencing host-pathogen interactions with respect to resistance and virulence structure. For ecotypes of the native Australian flax, *Linum marginale*, which is subject to attack by the rust pathogen *Melampsora lini*, analysis of the resistance structure of ecotypically different plant populations revealed that plants of one ecotype were generally susceptible to pathogen isolates taken from all sites but that plant hybrids exhibited resistance similar to that of plants from the more resistant population. Similarly, the virulence structure of rust isolates collected from the hybrid plant population was more similar to those isolates taken from the more resistant population than from the susceptible ecotype. In addition, plants from the more susceptible population had substantially higher survivorship than the resistant plants, regardless of where the plants were grown (in the susceptible, resistant, or hybrid zones). Those results suggest that the likelihood of differential gene flow and survival of resistant or susceptible plants of different ecotypes at least partially explains the maintenance of a relatively narrow hybrid zone (Carlsson-Graner et al. 1999).

Given the array of new ranges that introduced species might enter, it is worth considering briefly how ecological context can influence the speed of evolution. The rapidity with which a population can respond to selection will depend on the amount of additive genetic variation for fitness-related traits and the strength and direction of selection. Modern agricultural practices—in which the grower makes every effort to eradicate unwanted plants, often including nonindigenous plants—probably constitute some of the most intense selection pressures that introduced species encounter. Much of this selection can be quite consistent in direction, especially where monocultures are grown from year to year. There is good evidence that under these conditions such weedy (and usually nonindigenous) plant populations have responded through the evolution of locally adapted races that are specifically adapted to particular crops (Baker 1974, Barrett 1988). Indeed, many agricultural races of weeds (agroecotypes) are so specialized to the crop environment that they are rarely encountered outside the agroecosystems to which they have become adapted (Barrett 1983).

Among hosts and pathogens that have undergone coevolution, the pathogens may have an evolutionary advantage. In those cases, pathogen populations could be locally adapted, having higher mean fitness on sympatric than on allopatric hosts. Simple frequency-dependent selection models predict complex patterns of pathogen performance on sympatric and allopatric populations. With local extinction, recolonization, and gene flow in metapopulations, variable selection pressure and stochasticity could obscure local processes or change the extent to which local adaptation occurs. Alternatively, gene flow could introduce adaptive variation, and differential migration rates could modify the asymmetry of host and pathogen evolutionary rates (Koltz and Shykoff 1998).

Selection pressures encountered during the invasion of natural habitats are likely to be much more complicated than those which occur in agroecosystems. In particular, selection is likely to be less predictable and perhaps less directional. Diversifying selection would then be expected to maintain variation in populations, and the rapid evolution of specialized races of limited ecological tolerance would be less likely at least over short periods. Predicting the course of evolution in such biotically complex situations will be more difficult than in agricultural habitats, where growers strive for environmental homogeneity through the production of a uniform set of growing conditions for the crop.

KEY FINDINGS

- Some persistent nonindigenous species undergo a transition and become invasive. However, compared with the factors that govern arrival and persistence, there is considerable uncertainty regarding the biotic and abiotic factors that produce an invading population.
- The transition from established (or persistent) to invasive does not have a single explanation, but appears to be caused by the interaction of chance events in the new range, the biological attributes of the species, and the recipient community's composition.
- The history of a species' invasion in another location or country is often a useful predictor of its behavior in a new area.
- Many of the characteristics that determine establishment also are important in determining an invading population. For instance, a high reproductive or growth capacity and the availability of suitable habitats, resources, or hosts are important. It is not always known why a species with a moderate rate of population growth makes the transition to a very high rate of growth.
- Dispersal is clearly important in facilitating the transition to an invasion. Relevant dispersal components include the number of propagules available for movement, the opportunity for and mechanisms of dispersal, the distances that propagules are transported, and the spatial pattern of the dispersed propagules.
- Although some invasions advance as a continuous wave front, most advance spatially by establishment of some minimal number of widely separated foci. Establishment of multiple foci appears to be very important in triggering an invasion, regardless of the taxonomic group.
- Habitats and communities differ in their vulnerability to the entry of potentially invasive species. For example, arid or otherwise treeless communities appear more vulnerable to airborne plant dispersal than communities with a continuous forest canopy. In contrast, forest communities might be more vulnerable to animal-dispersed seeds and fleshy fruits. Sometimes, nonindigenous species

become invasive through their ability to tap resources unused or underused by native species.

- Biotic agents, including competitors and mutualists, play a role in the transition of an established species to a proliferating and spreading species. However, there appear to be no consistent relationships across groups (plants, arthropods, and plant pathogens).
- The roles of biodiversity and habitat disturbances in influencing species invasions are hotly contested. At best, conclusions depend on the invasive group.
- The genetic consequences of invasions vary widely among taxonomic groups. High genetic diversity of an established species is not a requirement for its transition to an invader. However, multiple introductions of a species into a new range often facilitate the emergence of new genotypes, some of which will have higher fitness than their parents. The result is an increased probability of yielding an invading population.
- Agricultural practices associated with a crop tend to provide intense and highly directional selection of invasive species which results in locally adapted races limited only by the area of the crop.

5

The Impact of Invasions

Harmful invasions are the outcome of a series of low-probability events. Williamson's "Tens Rule" (Williamson 1996) suggests that less than 1% of species that are introduced into a new environment will become damaging pests. Although organisms that arrive and establish themselves in a new range are positioned to have adverse effects on the surrounding flora and fauna, only a small fraction have been shown to do so, and that is true for both intentional and unintentional introductions. The ones that do become invasive can have, however, staggering economic and environmental costs. Economic costs—$137 billion/year by one estimate (Pimentel et al. 2000)—of invasions by species of plants, animals, and microorganisms generally do not include the displacement or extinction of native species that are of no immediate economic concern or the effects on native ecosystems, such as changes in fire regimes, nutrient cycling, or hydrology. Moreover, for every class of invasions, many effects probably go undetected or unmeasured. Because there are few resources available to combat damaging invasive species, it would be ideal to identify the most threatening organisms and the most vulnerable communities.

There is no uniform agreement among investigators in this field on how to judge the severity of an impact, partly because scientists have not been able to carry out comprehensive and carefully designed studies of invasions. Probably the best published data on establishment and impact of introduced species come from work on biological control, which is particularly relevant for assessing impacts in forest, range, and agricultural ecosystems because most biological control efforts on both islands and mainlands are in these ecosystems. Few generalizations related to predicting the magnitude of an invader's impact are accepted (Vitousek 1990, Parker et al. 1999, Simberloff and Von Holle 1999, Goodell et al. 2000). One is that, in the aggregate, impacts (however defined) are likely to increase with the number, geographic range, and abundance of the introduced species. Some support for that prediction comes from well-studied natural enemies released for biological control, in which suppression of target plant species increases with the number of control species established (Hoffmann and Moran 1998). A second is that the more geographically isolated the biota of a region is, the more vulnerable it is to invasion. The latter generalization is based largely on the conventional wisdom that oceanic islands are more easily invaded than mainland areas and that native species on oceanic islands are somehow more vulnerable than those on the mainland (Elton 1958, Carlquist 1965, Wilson 1965). The explanation for that vulnerability is that the descendants of the native species on islands experienced new colonization events infrequently and might have evolved in the absence of competitors, predators, or pathogens (Carlquist 1974). However, Simberloff (1995) finds little support for the conventional wisdom that islands are more easily invaded than mainland areas or that ecological effects of invasions are greater on islands than in mainland situations. Failed immigrations are often unrecorded, and claims that an introduced species has displaced a native one are often based on correlated population changes rather than experiment or detailed field observations. Species transfers from mainland to islands appear to be far more common than transfers from islands to mainland. In Simberloff's view, the data are inadequate to support conclusions about the invasibility or fragility of islands and mainland. A third generalization is that invaders likely to have impacts are those which create changes in disturbance regimes for which native species are ill prepared (Mack 1989): native species are especially likely to be adversely affected by the arrival of new immigrants because nothing in their evolution would likely have been comparable with the interactions suddenly faced.

Those generalizations do not identify specific potential invaders because they ignore mechanisms; the mechanisms of an invasion that threatens native species on islands are as varied as the characteristics of the invaders. For example, an invader might duplicate a functional role already played by resident species but be competitively superior in this role (Mooney and Cleland 2001), reducing the natives' role and threatening their existence. Or an invader could perform novel functions in its new community, as when a mammalian predator invades an oceanic island that lacks native mammalian predators (Elton 1958) or a nitrogen-fixing plant invades a region of nitrogen-poor soil (Vitousek et al. 1987, Vitousek 1990).

Although the mechanisms of invasions of an isolated biota are too varied and too poorly characterized to be applied elsewhere, the identification of the vulnerability of an isolated biota is, from a management perspective, a reason at least to take special precautions to keep nonindigenous species from proliferating there. The determination of measures for all aspects of the impact of invasive species would be useful in strengthening and focusing the ability to predict harm. This chapter reviews different scales of biological organization (individual, population, community, and ecosystem) in which impacts have been identified and discusses the development of methods to assess, quantify, and compare impacts.

DEFINING AND MEASURING IMPACT

There are few guidelines or widely accepted protocols for measuring the impact of an invader. Parker et al. (1999) suggest that the overall impact, I, of an invader on a geographic scale can be related to three factors: the total area occupied by the species, R; its abundance, A; and some measure, E, of the impact per individual or per unit of biomass. Impact can be represented as a linear combination of factors in the equation $I = R \times A \times E$. If a nonindigenous species is widespread and abundant, prediction and comparison of the impacts of invaders rest with forecasting the per capita effect, E.

Predicting invasions with that framework is fraught with obstacles (Parker et al. 1999). First, there are difficulties in measurement: per capita effects are harder to define and measure than abundance and range. Per capita effects resemble the coefficients linking interacting species in competition and predator-prey models (where the change in abundance of one species is linked to the abundance of another species via a coefficient symbolizing the strength of their interaction), but they are seldom measured in empirical studies. Second, R, A, and E are not independent. For example, it is well known from other contexts that local abundance is positively correlated with the area of an organism's range (Gaston et al. 1997, Holt et al. 1997). Patterns of correlation among R, A, and E and the underlying mechanisms that connect them warrant further investigation. Third, the functional form of the relationship among R, A, and E can be nonlinear.

Nonlinearities can arise, for example, if the per-unit effect varies with the density of organisms. Fourth, cumulative effects of multiple invasive species are not addressed in the framework; interactions among multiple species can be antagonistic, independent, or synergistic. A common form of synergistic effect arises from the intimate interaction between a plant and its fruit or seed disperser. An invasive plant could be spread widely if a nonindigenous bird or other frugivore were dependent on the plant's fruit or seeds. As the fruit-eater spread the plant, there would be more plants in new locales that could support more fruit-eaters, and so on. Synergistic interactions among invaders, in which one invader facilitates another, have been documented (Simberloff and Von Holle 1999). It is too early to claim any general patterns in the frequency of synergistic, independent, and antagonistic effects among invaders. As the numbers of invasive plants, animals, and pathogens in the United States continue to grow, their potential for interacting in expected and unexpected ways will increase.

Parker et al. (1999) review impacts of invaders at five levels of biological organization: effects on individuals (including rates of growth, development, birth, death, and movement), genetic effects (including hybridization), population dynamic effects (mean and variance in abundance, population growth rates, and so on), community effects (species richness, diversity, and trophic structure), and effects on ecosystem processes (primary or secondary productivity, hydrology, nutrient cycling, soil development, and disturbance frequency). From a sample of the literature on the impacts of invaders, Parker et al. (1999) recorded the number of published studies that produced quantitative data at five biological levels on five guilds of invading species: freshwater fish, freshwater invertebrates, marine invertebrates, algae and vascular plants, and insects and other terrestrial invertebrates. Population-level effects were the most frequently studied impacts. Studies of community-level impacts were common only for plants. The least-studied impacts, except for freshwater fishes, were genetic changes and long-term evolutionary effects.

Individual Effects

Invaders can have a variety of effects on the performance of individuals. For example, invasive plants can compete with native plants and reduce their growth (Gentle and Duggin 1997) and change their structure, such as rooting depth (D'Antonio and Mahall 1991). Invasive insects and pathogens can decrease hosts' rates of growth, development, survival, reproduction, and movement. Such changes in individual growth and life cycles can translate into changes in population size and fate. Population models built around a simple description of the life cycle can be used to link the individual and the population (Caswell 2000).

Genetic Effects

Nonindigenous species sometimes invade areas inhabited by closely related native species. If nonindigenous and native species interbreed, genetic exchange between the two species can alter the genetic makeup of native populations. Such hybridization between an invader and a native is common and can have several consequences, including the spawning of new invaders (Rhymer and Simberloff 1966). Repeated hybridization of North American cordgrass (*Spartina alterniflora*) with British native cordgrass (*S. maritima*) eventually yielded a new, highly invasive species, *S. anglica* (Thompson 1991). Production of hybrid swarms and widespread introgression can lead to virtual extinction of native taxa through a swamping of their original genomic makeup through recombination with genes of the invader (Rhymer and Simberloff 1996), especially if the invader becomes much more common than the native species; this seemingly hypothetical threat is both real and serious: three species federally listed as endangered in the United States have gone extinct since enactment of the Endangered Species Act because of hybridization with nonindigenous species (McMillan and Wilcove 1994). Finally, hybridization among plants may spawn invasion by plant pathogens.

According to the "hybrid bridge hypothesis", hybrid plants that are morphologically, genetically, and spatially intermediate between parent species can make it easier for pathogens to acquire new hosts (either by direct transfer to hybrids or indirect transfer to new hosts using hybrids as a "stepping stone") (Floate and Whitham 1993).

The addition of novel, including invasive, organisms in new ranges creates opportunities for evolution and makes prediction of impacts more difficult. Adaptations arising in plants when they move to new environments can produce invasive descendants. The tropical alga *Caulerpa taxifolia* evolved tolerance of low temperatures through its cultivation in an outdoor tank at the Stuttgart Zoo (Meinesz 1999). Evolution in native animals in response to the entry of invaders can make it difficult to restore the web of interactions characteristic of the native community. For example, the native checkerspot butterfly *Euphydrias editha* evolved a change in host preference from a native to an introduced plant in response to a decline of its native host and an increase of a novel, invasive host, *Plantago lanceolata* (Singer et al. 1993). By the time the native host is restored to its original abundance, if ever, the insect population might have lost the capacity to use it.

Introduced biological controls can become less effective because of evolved changes in the virulence of control organisms or changes in the resistance of target organisms. *Myxoma* virus was released in Australia to control the introduced European rabbit *Oryctolagus cuniculus*. Within a few years, the virulence of the virus had declined, and the resistance of the rabbits had increased sharply (Dwyer et al. 1990). In other cases, nonindigenous biological control organisms appear to become more effective by adapting to novel hosts. An ichneumonid parasitic wasp, *Bathyplectes curculionis*, imported to the United States to control the alfalfa weevil, *Hypera postica,* was originally ineffective against the Egyptian alfalfa weevil, *Hypera brunneipennis*. Initial dissections showed that 35-40% of the wasp's eggs were destroyed by the immune response of the larval weevil, whereas samples taken 15 years later showed only 5% egg loss (Salt and van den Bosch 1967).

Evolutionary adjustments of control and target organisms in biological control programs are not well known, but in documented cases in other contexts invading organisms have adapted to their new environments and organisms have adapted to new invaders (Mooney and Cleland 2001). Huey et al. (2000) demonstrated that introduction of a new fruit fly into the West Coast of North America resulted in the evolution, in only 20 years, of an apparently adaptive cline related to wing size throughout the fly's vast new latitudinal range extending from southern California to British Columbia. The cline that developed in North American female flies was similar to that found in the European native populations. The developmental basis of the cline of wing size was different between the European flies and the invader in North America, although the functional result was the same and provided additional evidence of the adaptive advantage of this set of traits. Cody and Overton (1996) described the reduction in dispersal ability for wind-dispersed seeds of invasive species onto islands in just a few generations in small isolated populations. Carroll and Dingle (1996) indicate that populations of the soapberry bug (*Jadera haemotoloma*) have evolved differing beak lengths in response to the introduction of new invasive hosts within only 50 years and Singer et al. (1993) have shown rapid evolution in the feeding preferences of the *Euphydryas* butterfly for the invading herb *Plantago lanceolata* in only 10 years. Thus, there are many cases of evolution both in invading species and in the species affected by invaders.

As noted earlier in this report, the ability of pathogens to adapt to different plant genotypes has been studied in detail, and the resulting knowledge has helped in forecasting the fate of new microbial genotypes in the environment (Mundt 1995). Fungal, bacterial, and viral plant pathogen populations evolve quickly to overcome resistance genes in hosts. For example, the average useful life of race-specific genes for resistance to fungal rusts of wheat has been estimated to be only 5 years (Mundt 1995).

Population and Community Effects

Invaders can cause reduction in the biological diversity of native species and the size of populations; next to land transformation, they are the most important cause of extinction (Vitousek et al. 1996). After habitat destruction (which affects 81% of imperiled plant species), introduced species contribute more to the imperilment of species (57%) in the United States than the next three causes combined—pollution (7%), overexploitation (10%), and disease (1%) (Wilcove et al. 1998, 2000) (Categories are nonexclusive and do not sum to 100%). Replacement of natives with nonindigenous species is immediate, readily measurable evidence of the impact of invasions.

Extinction could be the most dramatic impact of invasive species. Small populations of natives suffer the highest risk of extinction from various genetic and demographic causes discussed earlier in this report in connection with the same hazards that small immigrant populations experience. Invaders pose a major risk to threatened and endangered species: about 400 of the 958 species that are listed as threatened or endangered under the Endangered Species Act are considered to be at risk primarily because of competition with or predation by nonindigenous species (Wilcove et al. 1998, Stein et al. 2000). Invaders can also interact with habitat transformation and thus exacerbate the threat to biodiversity (Hobbs 2000).

Extinction of native species, although dramatic, actually characterizes relatively few invasions (Simberloff 1981). Reduced population sizes and local extirpation of a species appear more common than global extinction of a species, but changes in population sizes of native species after invasion by nonindigenous species can vary greatly in magnitude and even direction. For example, establishment of immigrant ladybird beetles *Coccinella septempunctata* and *Harmonia axyridis* appears to be associated with declining populations of some native ladybird beetles and potentially will alter predatory communities in forest-agriculture interfaces (Colunga-Garcia and Gage 1998, Howarth 2000). Invasion by the fire ant *Solenopsis invicta* Buren has dramatically reduced the native ant fauna. In a detailed study in Texas, species richness of ants in infested areas decreased by 70%, and the number of native individuals dropped by 90%. Competitive displacement appears to be the primary mechanism. Similarly, overall non-ant arthropod diversity was reduced by 30%, and the numbers of individuals by 70% (Porter and Savignano 1990). The fire ants excluded some native species from the invaded areas, but it is noteworthy that the natives persisted in nearby uninvaded areas and that no extinctions were observed.

Predictions of loss of regional biodiversity accompanying plant invasions have been based on observations of diversity decreasing with the extent of an invasion. For example, the impact of nonindigenous plants on native plants has been documented for fynbos vegetation on the Cape Peninsula in South Africa. This ecosystem supports 2285 native plant species (Trinder-Smith et al. 1996), including 90 endemic taxa (comprising species, subspecies and varieties) (Richardson et al. 1996). Richardson et al. (1989) showed that invaded sites of the fynbos biome have fewer than half the plant species of matched uninvaded sites. Holmes and Cowling (1997) provided similar evidence: invaded sites had 60-86% fewer plant species. *Mimosa pigra* in northern Australia converted hundreds of thousands of hectares of open sedge wetland to shrubland, and native plants and animals were lost (Lonsdale 1993, Braithwaite et al. 1989). The Brazilian peppertree (*Schinus terebinthifolius*) was introduced to Florida in the late 19th century. It became widespread in the early 1960s and today is established on over 280,000 hectares in south Florida, often in dense stands that exclude all other vegetation (Schmitz et al. 1997).

Some functional groups are sensitive to the presence of nonindigenous plants, and others are remarkably resilient (Holmes and Cowling 1997). The chestnut blight fungus arrived in New York City in the late 19th century on nursery stock from Asia and in less than 50 years had spread over 90 million hectares of the eastern United States, destroying virtually every American chestnut tree (*Castanea dentata*). Because chestnut had made up one-fourth or more of the canopy of tall trees in many forests, the effects on the entire ecosystem might have initially been thought to be staggering (Roane et al. 1986). But other species (*Quercus* and *Carya* spp.) replaced chestnut in the canopy, leaving few notable changes in some ecosystem characteristics, such as primary productivity and hydrology, despite striking changes in other attributes, including the structure and dynamics of food webs and the social, cultural, and economic life of people (Youngs 2000). The simplification of ecological communities might make them more vulnerable to invasion (Levine 2000) or render them less stable or predictable in species composition (Tilman 2000). In extreme cases, invasive species may so reduce native species richness that the original native community no longer exists and has been supplanted by a new community dominated by one or more invasive species. Even the emergence of the new community does not guarantee the end of alteration. In the western United States the once dominant role of *Bromus tectorum* is being reduced locally through the more recent invasion of *Centaurea solstitialis*. Thus, one invader is being supplanted by another (R.N. Mack, personal observation).

In native forest ecosystems, insects and microorganisms are intrinsically involved in such processes as decomposition and nutrient cycling, maintenance of forest productivity, pollination, and food webs (Mattson and Addy 1975, Haack and Byler 1993, Gilbert and Hubbell 1996). Their influence on forest composition and structure occurs on genetic to landscape scales, but these organisms have evolved with their ecosystems over *long* biological periods. In contrast, introduced insects and microorganisms have no evolutionary history with the forest ecosystems that they have come to influence. Even though most foreign invaders are similar to indigenous organisms in how they feed or infect their hosts, the ecological changes that have resulted have been dramatic and cascading and have occurred over *short* periods (Gibbs and Wainhouse 1986, Oak 1998).

For example, forests since the invasion of the chestnut blight have often been dominated by oak species. Their increased abundance and continuity now provide ideal hosts for the introduced gypsy moth; for the increased expression of oak wilt, an indigenous vascular disease; and for drought-related declines (Liebhold et al. 1995, Simberloff 1996). Likewise, beech bark disease, caused by a nonindigenous scale insect and a pathogen, has led forests once composed of beech thickets or sites to be transformed to grass or shrub land–a change that can alter fire regimes (Oak 1998). Both maladies have affected wildlife populations that depend on beech nuts (Martin et al. 1961). A nonindigenous foliage feeder such as the gypsy moth may function like a native defoliator and appear to have minor effects on the forest, but the consequences of invasion include cumulative stresses on the host and alteration of the populations of other native herbivore species, and these effects can extend to other trophic levels.

What might be the ultimate, global result of mixing of the world's biota? Brown (1995) has estimated, on the basis of species area relationships for continents, the worst-case scenario for the impact of free exchange of biotic material across former biogeographic barriers. The estimate assumed that continental drift could be reversed and that all the earth's land could be reassembled in a single giant continent, but with the current climates and geological features intact. With these assumptions, there would be a massive decrease in species—65.7% in land mammals, 47.6% in land birds, 35% in butterflies, and 70.5% in angiosperms. Brown tempered that pessimistic assessment with a number of caveats. Colonization and expansion of ranges must ultimately decrease global diversity, but they tend in the short term to increase local diversity. The extent of the biotic enrichment varies, but many countries have 20% or more nonindigenous species in their floras (Vitousek et al. 1996). Deliberately introduced species can play a role in the maintenance and management of ecosystem processes. Examples of such species are natural enemies of pests for biological control; aesthetically pleasing, fast-growing, pollution-resistant horticultural plants; fish communities in reservoirs; and grasses that can reclaim strip-mined land in arid regions. The danger arises from nonindigenous species that either play no constructive role or play unexpected roles in their new ranges.

Ecosystem Effects

Invaders that affect ecosystem processes—such as productivity, nutrient cycling, or disturbance regimes—have been viewed as the most difficult to quantify and verify (Vitousek and Walker 1989, Mack and D'Antonio 1998). In a sense, changing ecosystem processes "changes the rules of the game" in a way that influences many, if not all, of the component species. Plant invasions can also alter nutrient-cycling patterns, as illustrated by the invasion of the nitrogen-fixing tree *Myrica faya* on volcanic surfaces in Hawaii (Vitousek and Walker 1989). The invasion of American rangelands by *Bromus tectorum* (cheatgrass) has increased the frequency and intensity of fires, thereby transforming steppe once dominated by the shrub *Artemisia tridentata* (big sagebrush) to annual grasslands (Whisenant 1990). Similarly, the invasion of nonindigenous annual grasses into Californian chaparral has resulted in more-frequent and more-intense fires, which in turn have altered species composition (Zedler et al. 1983). Plant invasions can also alter hydrology, as illustrated by Melaleuca (*Melaleuca quinquenervia*), which increases soil elevations and thereby has influenced the hydrology of Florida wetlands (Schmitz et al. 1997), and by the invasion of *Pinus* spp. into the South African fynbos, which has radically reduced the water yield of catchments (Le Maitre et al. 1995). A recent review (Parker et al. 1999) indicates that most studies of the impacts of invaders on ecosystem processes have concentrated on the effects of the plants—through uptake of light, nutrients, or water—on other plant species. Native animals are also affected by plant invaders (Braithwaite et al. 1989), through loss of habitat and loss of food resources; these interactions have been little studied and might well be underestimated.

An invader would have substantial social or economic effects if it altered "ecosystem services" (cf. Ehrlich and Mooney 1983), such as maintaining the gaseous composition of the atmosphere, controlling regional climates, generating and maintaining soils, controlling floods, disposing of wastes, recycling nutrients, and controlling pests (Ehrlich and Wilson 1991). A potentially global change is under way through the conversion of much of the forested Amazon drainage to grasslands. Huge swaths of tropical forest continue to be cleared, burned, and sown with nonindigenous grasses. These grasses, such as *Melinis minutiflora* and *Brachiaria* spp., which were introduced primarily from Africa, are forming a variety of new communities: some appear to require continual cultivation, and others escape cultivation and are forming invasions. In either case, aggregate effects of the grasslands have enormous impact on the composition of greenhouse gases in the atmosphere and alter the light regime (reflectivity and energy balance) and hydrology in their region and beyond (Mack et al. 2000, Williams and Baruch 2000 and references therein). Perhaps nowhere else on the earth are invasive species altering the biosphere to the same extent, but similar regional transformations are simultaneously occurring elsewhere. The spreads of the invasive *Pennisetum ciliare* (buffelgrass) in Mexico (Burquez and Quintana 1994 as cited in D'Antonio 2000), of *Imperata cylindrica* (alang alang) in the tropics and subtropics (Lippincott 2000), and of *Pennisetum spp*. in Madagascar (P. Binggeli, personal communication) are examples of the replacement of forest or parkland communities with invasive grasses.

The value of lost ecosystem goods and services is often not recognized, because they are not traded on financial markets. But these commodities and services, which are assumed to be available free for all, are under threat. Some progress is being made in calculating the value of ecosystem goods and services and using this information in environmental decision-making and economic policy (Daily et al. 2000). The connections between biodiversity, ecosystem services, and human health must be better understood before a predictive theory of invasion impacts can be developed.

Cumulative and Indirect Effects

The adverse effects of a single invasive species can be small, but the aggregate effects of multiple invasive species can be large. Indirect effects occur when one species influences another via intermediate species, as when two species interact via a shared natural enemy or a shared resource. Interactions among gypsy moths, mice, and Lyme disease in eastern North American oak forests (Elkinton et al. 1996, Jones et al. 1998) illustrate the cascading direct and indirect effects that can occur when communities are tightly linked. In central Massachusetts, oak trees, the preferred host of gypsy moth larvae, produce large acorn crops every 2-5 years. Acorns are an important winter food source for mice, and mice density increases after heavy acorn years. Mice and deer are the primary hosts of the black-legged tick, *Ixodes scapularis*, which is the vector of the spirochete bacteria, *Borrelia burgdorferi,* that causes Lyme disease in humans. Heavy defoliation during gypsy moth outbreaks reduces the vigor of oaks, and that results in decreased acorn production, which in turn leads to lower density of mice, which are important predators of gypsy moth pupae in New England. Researchers found that increased abundance of acorns was associated with lower gypsy moth survival but higher densities of mice and host-seeking deer ticks, which presumably increase the incidence of Lyme disease. Such chain reactions are difficult to identify, let alone predict or manage. Moreover, these interactions can vary spatially or temporally. In West Virginia, where gypsy moth populations have only recently become established, there was no association between abundances of small mammalian predators and gypsy moth dynamics (Grusheky et al. 1998).

The composition and structure of North American forests have always been in flux as they are continuously affected by biotic and abiotic agents. Human activities associated with settlement over the last 400 years have been some of the most pervasive forces in shaping the forests that exist today (Franklin et al. 1987, Merrill 1996). Among those activities have been logging and agricultural practices and the fires that were used to aid hunting and the preparation of land for farming. As the primeval forests were felled, their diversity, composition, and complexity were greatly altered. The forests that have regenerated represent the cumulative effects of the various disturbance agents and are the forests into which most invasive organisms have been introduced (Cronon 1983).

Insects and pathogens historically were viewed as two of the most important damaging agents with respect to forests (Hepting and Jemison 1958). Attempts to eradicate or suppress their outbreaks were initiated when pests produced effects that were in conflict with wood and fiber production, destroyed wildlife habitat, or interfered with natural resources that have been aesthetically valued by humans. More contemporary views have recognized insects and pathogens as normal forest ecosystem components. Their roles as recyclers of carbon and other nutrients, as pollinators and plant symbionts, as food sources for vertebrates, invertebrates, and other microorganisms, and as creators of habitat for wildlife are well summarized (Haack and Byler 1993, Gilbert and Hubbell 1996). In contrast, introduced insects and pathogens are not normal components of the ecosystems that they have come to influence. The general view is that invasive insects and microorganisms are not regulated by the co-evolved resistance mechanisms in their hosts or by the parasites, predators, and diseases that regulate them in their native ecosystems (von Broembsen 1989). All too often, the impact of an invading species has been viewed narrowly as causing extensive mortality and growth loss in the affected species. In reality, the ecological changes that have resulted from their damage typically set off a cascading chain of events that has resulted in rapid ecosystem changes.

A brief examination is warranted of how chestnut blight and gypsy moths have created cascading events to alter forest organization rapidly. Chestnut blight resulted in the most profound set of changes ever recorded in a North American forest ecosystem. The causal fungus, *Cryphonectria parasitica* is native to East Asia; after its early-1900s discovery in North America, it proceeded to infect and kill American chestnut trees, which once made up 25% of the eastern hardwood forest (Liebhold et al. 1995). As the chestnuts died, the newly available space was occupied by middle-story and understory species, including oak. Fire disturbances before the blight had given oaks an early advantage over light-seeded, less-fire-tolerant, thinner-barked species such as maple and yellow poplar (Stephenson 1986, Oak 1998). As the forests with emergent oaks have matured, they have been subject to oak decline, a condition that appears to develop as physiologically mature trees experience insect defoliation or drought (Houston 1987). Although the native insect defoliators, such as elm spanworm (*Ennomos subsignarius*), have been implicated in this decline, the introduced gypsy moth (*Lymantria dispar*) has been the most important agent of damage. Gypsy moth defoliation disturbs the carbohydrate physiology of oak root systems and makes them highly susceptible to native root-invading fungi (*Armillaria* spp.) and insects, particularly the two-lined chestnut borer (*Agrilus bilineatus*), a root collar insect (Houston 1987, Oak 1998). As the gypsy moth has continued its spread southward and westward from New England through the Appalachians, the oak decline-gypsy moth situation has resulted in significant oak mortality. Species that have replaced oaks include more-shade-tolerant trees, such as black gum, red maple, white ash, and yellow poplar. Oak mortality has created dens for wildlife and increased the amount of coarse woody debris. The forests that eventually emerge from the impact of chestnut blight and gypsy moth defoliation may be more tolerant to oak decline and defoliation but will be structurally and compositionally very different plant and animal habitats.

Two other nonindigenous organisms, a scale insect (*Cryptococcus fagisuga)* and a fungus *(Nectria coccinea* var. *faginata)*, are influencing the eastern forests of North America as they operate in concert to cause beech bark disease (Houston 1994). The small scale insect creates tiny feeding wounds in the thin bark of beech, which are colonized by the fungus. Eventually, mature beech trees die as the many fungal infections coalesce and girdle the tree. The killing front of this insect–pathogen complex has spread from the introduction point of the scale insect in Nova Scotia to central Pennsylvania; small outbreaks of the disease now occur as far south as the Great Smoky Mountains National Park. The dynamics of beech bark disease begin as infestations by the scale insect and fungal infections of the bark occur along the killing front. As native beeches dies, the remaining beech trees are riddled with nonlethal infections that grotesquely deform them. Further deaths lead to the development of beech thickets that arise from root sprouts. General structural changes in the forest include loss of beech in the canopy, increased snags and downed woody debris, and overabundance of infected beech stems. Long-term effects of the elimination of beech are uncertain, but some stands are already being replaced by sugar maple and yellow birch or have been transformed into grasslands or shrub lands (Oak 1998). Although American beech is not highly prized economically, it had a valuable wildlife role in producing beechnuts, an important food for some birds, squirrels and chipmunks (Martin et al. 1961).

Evaluating Impacts on Communities

There is a fundamental need to identify common standard measures of impacts that would create a more reliable basis for comparison, interpolation, and extrapolation. What does a reduction by 20, 50, or even 75% in the fitness of a native species mean to its role and persistence on the site, and can these metrics be made meaningful across vastly different taxonomic groups? Similar questions have yet to be addressed about invader-caused alterations in nutrients, water availability, and other ecosystem components. The development of standard approaches to evaluating the impacts of invaders will strengthen future predictive efforts.

The chief reason for the difficulty in evaluating the impact of invasions, however, is the lack of sufficiently detailed data on the species composition, structure, and function of ecosystems before they are invaded. That is clearly the case with the introduction of the chestnut blight fungus: the only information that exists about preblight forests is anecdotal or comes from postblight studies (Stephenson 1986). There can be a long period between an introduction and the spread of an invader (Kowarik 1995). As a result, we recognize that an invasion has occurred only after the ecosystem has changed. The invasion of *Bromus tectorum* in the western United States, for example, occurred long before the identification of the native plant colonizers that *B. tectorum* supplanted (Mack 1988). The invasion process is a moving picture, but often we must rely on snapshots that relate spatial variation in structure and function of ecosystems to the abundance of invaders if we are to infer which ecosystem services could be lost as the invasion progresses. Increased availability of data on the composition of natural ecosystems at all levels of complexity would help substantially.

Both the invader and the recipient ecosystem are likely to change. Some invaded systems settle to a new equilibrium; others undergo sustained "boom and bust" oscillations. Some invaders impose constant effects; the effects of others are more dynamic. For example, planned introductions of "predators" for control of arthropods and weeds show a wide range of dynamic behaviors (Hassell 1978): some predators have little detectable effect on their prey's dynamics; in other interactions, the predators clearly are maintaining their prey at very low equilibrium densities; a few predators and their prey undergo cyclic oscillations; and some interactions are characterized by episodic prey outbreaks when predation ceases to be limiting.

A general increase in the temporal and spatial scale of invasion studies is needed to quantify explicitly cases among each of these categories. For example, large-scale studies are needed to incorporate background variations in response variables and to incorporate variations in changes associated with invasion that are not captured by small-scale studies. One approach is to construct matrices that describe the variances for each species in an ecosystem along the diagonal elements and the covariances between the population sizes of all pairs of species across the off-diagonal elements—at least one matrix for the variances and covariances before the invasion and one for after it (Parker et al. 1999). Comparisons of the changes in such matrices could provide a description of changes in the structure and dynamics of an invaded community.

BOX 5-1 Impacts of Invasive-Species Management Efforts

In the rush to control invasive species, we sometimes create long-term problems that are harder to address. Importation of nonindigenous predators, parasitoids, or pathogens to control invasive pests can have long-term deleterious effects on native, nontarget species. *Compsilura concinnata* was intentionally established for gypsy moth control in North America. This parasitic fly is known to parasitize over 180 native lepidopteran species; it might be responsible for dramatic declines of large attractive species, such as the cecropia moth (Boettner et al. 2000), and it has expanded well beyond the range occupied by gypsy moths.

Similar examples of unanticipated effects on nontarget species have been documented for insects introduced for biological control of undesirable plants. The European weevil *Rhinocyllus conicus*, introduced in 1968 to control weedy thistles, now affects native nontarget plants, including rare species of Californian *Cirsium* (Ehler 1991, Louda et al. 1997). An Argentine moth, *Cactoblastis cactorum*, was introduced into the Caribbean in 1957 to control undesirable *Opuntia* species. Its unanticipated arrival in Florida in 1989, however, has generated concern about its impacts on five native *Opuntia* species, including a rare, protected cactus. Continued range expansion threatens the diverse guild of *Opuntia* in Mexico (Johnson and Stiling 1996, Pemberton 1995, Simberloff 1992, Strong and Pemberton 2000). Two immigrant ladybird beetles, *Coccinella septempunctata (L)* and *Harmonia axyridis (pallas)*, originally imported for biological control, are suspected of displacing native ladybird beetle species (Colunga-Garcia and Gage 1998), and *H. axyridis* is now considered an annoying pest because it aggregates in masses on homes.

A further complication arises when an invasive species is deemed a curse by one segment of society and a salvation by another. That possibility is well illus-

We are unlikely to obtain such quantitative information on patterns of variation and correlation among abundances of species in a community, so it is reassuring that simple qualitative analysis and modeling can further our understanding of potential ecological effects of nonindigenous species and serve as a practical tool for adaptive management (Li et al. 1999). A community matrix can be constructed by representing relationships between the species (or variables) in a community with scores of positive (+1), negative (-1), or zero values, signifying the effect of one species or variable on another. Mathematical tools can be applied to determine the presence of equilibrium and its stability, as well as the effect of input into the system. This approach has led to important policy and management recommendations in agriculture, and fisheries, and has been useful in risk analysis of species introductions.

trated by the protracted legal battles in Australia over *Echium plantagineium,* given the antithetical sobriquets of "Patterson's Curse" and "Salvation Jane" (Parsons and Cuthbertson 1992)! A similar situation may yet arise in the United States over the herbaceous species *Hypericum perforatum* (St. John's wort). It is unquestionably an aggressive rangeland weed and was the target of a successful biological control program (Huffaker and Kennett 1959). But today the plant is valued by some as an herbal remedy and is touted as a boon to some local economies.

Furthermore, the "zero-tolerance" policies used by many regulatory agencies might require pesticide applications, inspections, or other treatment before plant material from areas known to be infested by a nonindigenous insect or pathogen is permitted to enter uninfested areas. Such policies are incompatible with biological control, nullify economic injury or action thresholds that are integral components of integrated pest-management programs, often lead to increased pesticide use, and can result in considerable costs to producers, inspection agencies, and other officials in affected areas.

Even attempts to disrupt the life cycle of the nonindigenous pest without classical biological control can have environmental consequences. For example, establishment of white pine blister rust had profound ecological impacts in many northern states, but the effects of programs to eradicate the native *Ribes* species (the alternative host of the pathogen) and discourage regeneration of white pine have not been addressed.

Collectively, those examples show the need for careful evaluation of biological control agents, inasmuch as protocols for screening the evolutionary potential of invaders–weighing genetic variation, natural selection, and ecological opportunity—are still in early stages of development (Ewel et al. 1999). The potential for such unintended consequences and the public's diverse reaction to nonindigenous species need to be assessed as much as possible before the species' release.

KEY FINDINGS

- Of the country's persistent nonindigenous species, only about 10 % are considered invasive. But appearances can deceive, and many of the remaining 90% might be considered innocuous only because their harmful effects have not been documented or even investigated.
- Effects or impacts of invasive species are often hard to measure and even harder to predict, because scientific uncertainty arises in quantifying each step in the invasion process. Moreover, data are lacking on species composition and species abundance in many ecosystems before the arrival of invasive species.
- Impacts occur on various scales—biological, spatial, temporal. Effects become harder to predict as one moves from the individual to the genetic, popu-

lation, community and ecosystem levels. Long-term evolutionary and community effects are the least well studied and perhaps the least predictable. Furthermore, there are few widely accepted measures of the impact of invasive species.

- Classification of organisms by functional groups might help in predicting impacts. Among invaders, grasses that produce massive amounts of combustible fuel, plants that form mutualisms with nitrogen-fixing bacteria, and trees that produce dense, light-diminishing shade can have huge impacts in ecosystems in which these functional groups had been absent or their effects have been negligible.
- Invasive species often exert their influence by initiating a cascade of changes in the biotic and abiotic components of the ecosystem; examples are chestnut blight and gypsy moths in eastern North America.
- Some plant invasions, such as in the Amazon watershed, are becoming so extensive that they are probably affecting global atmospheric circulation and the global carbon budget.
- Few studies have been conducted on large temporal and spatial scales. Such studies could incorporate background variations in invasion-associated changes that are not captured by small-scale studies.

6

Evaluating Predictive Systems

The ability to identify potentially invasive species could yield enormous benefits. Quarantine measures could be streamlined to search primarily for designated species at points of entry, and detection efforts within the United States could be focused on the habitats in which the species are likely to reside. Such identification ability would replace the searches for often vaguely defined threats (poorly characterized invasive species) with searches for organisms that are of legitimate cause for concern and action.

A determination that a given nonindigenous plant or plant pest has the potential to become invasive in the United States presumes that information about it and its introduction are known, such as its characteristics; the specific event that brings it into the United States; where, when, and how it is brought in; that it can become established, proliferate, and spread in its new environment; and the harm it would do. The same criteria apply to nonindigenous organisms introduced as biological control agents (Strong and Pemberton 2000).

Prediction in this sense is not explanation. Explanation identifies why a phenomenon or event has occurred; in science, explanation is often based on statistical analysis of experimental observations. Much of the material in Chapters 2-4 is a review of factors that explain, to various extents, why some organisms are able to persist and spread, outcompete natives, and alter ecosystems. In contrast, prediction is the generation of statements about the likelihood that events will occur (Williamson 1996).

The committee concluded that a scientifically based system to predict invasiveness must satisfy three general criteria:

1. It must be transparent, be open to review, and have been evaluated by peers.
2. It must have a logical framework that includes independent factors—identified through critical observation, experimentation, or both—important in the invasion process.
3. Use of the framework must be repeatable and lead to the same outcome, regardless of who makes the predictions.

This chapter examines approaches for predicting the invasiveness of plants and the arthropod and pathogenic pests of plants in the United States. Most predictive systems rely principally on observational data (sometimes coupled with traits, origins, and the like). The data may be grouped taxonomically on coarse or fine levels (for example, all plants, animals, or microorganisms; or according to family, genus, or species), by characteristic (such as reproductive mode, mode of propagation, or environmental range), or by locale and climate of origin. The committee suggests a broader framework for organizing information used in predictive systems; the framework is based on the sequential steps of invasion: arrival, persistence or establishment, and proliferation and spread.

This chapter also addresses systems of prediction that are augmented by an assessment of the value or character of invasions and an assessment of the certainty of or confidence in their occurrence. Predictions based on this broader dimension of information and analysis are risk assessments, specifically ecological risk assessments.

Predicting biotic invasions has been based largely on identification of species that already have a record of invasiveness. This approach seems almost obvious, especially for plant pathogens. For example, the fungal pathogens of cereals are equally likely to be infectious on a given wheat variety in the United States, in Australia, and in western Europe. It would be imprudent to assume otherwise unless there were specific information to the contrary. Similar examples occur for arthropod pests. Even though the Russian wheat aphid has not yet produced the devastation in the United States that it produces elsewhere, it is a pest of wheat in many new ranges (Hughes 1996). No prolonged monitoring was deemed necessary to enforce control of the aphid once it appeared in the United States. Plant species known to be invasive have routinely sparked awareness of their invasive potential in unexploited new ranges. *The World's Worst Weeds*, the compendium by Holm et al. (1991), is empirical testimony to the recurrence of some species as invaders in many ranges. The first detection of one of these species in a new range should spark immediate eradication efforts. The record of a plant's invasiveness in other geographic areas beyond its native range remains the most reliable predictor of its ability to establish and invade. The same is true for arthropods and pathogens if host plants they can use elsewhere also occur in the United States.

Expert judgment of a species' history in new ranges has several limitations. First, expert judgment is subjective and given the same information, experts' evaluations of the threat of an invasion can differ. Second, some species considered potential invaders in the United States simply on the basis of their record elsewhere have yet to become problems here despite their repeated entry (Reed 1977). The failure so far to be a problem has multiple potential causes. On the basis of the information in Chapters 3 and 4, it is apparent that there is a high degree of stochasticity in the outcome of any immigration. A species with a record of invasion could eventually become invasive in an additional new range once stochastic forces were overcome or avoided. Finally, a further dilemma is posed by arthropod and plant pathogens that cause little or no recognizable damage to plants in their native habitats and therefore have been ignored but have the potential to cause substantial damage to those plants' susceptible North American relatives.

PREDICTION BASED ON CLIMATE-MATCHING

Even before ecology was formalized as a science, the ability to predict the geographic and ecological ranges of species by using climatic similarities was actively sought (von Humboldt and Bonpland 1807, Grace 1987). The extension of this reasoning to predict the potential new range of an introduced species and even whether it would survive at all in a new locale has long been practiced (Johnston 1924, Wilson et al. 1992). Such reasoning is supported by comparison of the climates in native and naturalized ranges for some species. Most striking in this regard is the extensive list of plant species that are native along the border of the Mediterranean Basin and are now naturalized in locales with climates similar to the Mediterranean Region: coastal areas of southern California and Chile, southwest Australia, and the Cape of Good Hope. Furthermore, species from each of the other four regions have become naturalized in one or more of the others (Kruger et al. 1989, Fox 1990).

There have been repeated attempts to develop "climate-matching" models by comparing the voluminous records of the earth's climates collected at numerous locations (Busby 1986, Panetta and Dodd 1987, Panetta and Mitchell, 1991, Cramer and Solomon 1993). The challenge (aside from verifying the accuracy of data from meteorological stations scattered around the globe) has been to integrate these data in an ecologically meaningful way. More important, weather is the stochastic expression of climate, and the persistence of organisms, whether native or introduced, is much influenced by this variation about the mean characteristics of any climate (Mack 1995).

CLIMEX is one example of the models developed to predict the potential ranges of introduced species (Sutherst et al. 1999). The model in its revised forms has been used repeatedly to predict the geographic distributions of plants, microbial pathogens, and arthropods under both current conditions and global climate-change scenarios (Sutherst et al. 1989, 1998, 1999). Its most extensive applications have been useful for predicting the fate of immigrant species that are candidates for release in biological control (by identifying possible sites to collect biocontrol species and sites where they might be released and persist), and in predicting the fate and new ranges of introduced pests (Sutherst 1991a,b).

In its basic composition, CLIMEX contains an open-ended meteorological database of about 2500 locations that span the world. Meteorological data include average monthly maximal and minimal temperatures, relative humidity, and precipitation. The model interpolates monthly average climatic data into weekly values. CLIMEX has two main operating modes: "Match Climates" and "Compare Locations". The "Match Climates" mode compares meteorological conditions among locations without reference to species. Either a specific meteorological variable (such as minimal winter temperature) or a suite of meteorological variables can be compared between locations for a specific period or the entire year. The model allows users to search the meteorological database in asking "Does Location X [a potential new locale] have a climate similar to that of Location Y [a species' native or other locale] under preset standards of similarity?" That basic task is common to many climate-matching software programs (Kriticos and Randall 2001).

The "Compare Locations" function is more applicable to the common need in predicting future invaders: it is used to predict potential distributions of species under current climatic regimes. Predictions are based on the climate in a species' current range, on experimentally determined tolerances of a species with respect to key environmental characteristics (for example, Vickery 1974), and on life-history information, such as senescence or diapause. Information on a species is used to find other locales in which the species potentially could persist.

A major limitation in the use of climate-matching (to compare a current range with a potential range) as a predictor of a species' potential new range(s) lies in the assumption that climate is the main, if not the only, determinant of a species' distribution. Distributions are also strongly influenced by the biotic component of any environment (Crawley 1992, Mack 1996a) and by chance dispersal; that is, a species might be absent from a locale (even in the general native range) through the vagaries of species dispersal rather than through environmental limitation (Sutherst and Maywald 1985, Davis et al. 1998). Furthermore, this system does not attempt to measure the impact of a species in its new range.

In addition, some species' distributions are comparatively uniform or at least quite narrowly defined: the climatic range that they can tolerate is not reflected in their native or current new distributions. For example, *Sorghum halepense* (Johnson grass) has extended its range into southern Canada, thereby far exceeding the climatic range that would have been predicted for it by considering its native subtropical range (Warwick et al. 1984). Such complications diminish or at least complicate predictions made by climate-matching models (Sutherst et al. 2000).

Furthermore, climate-matching programs rely on comparing average meteorological data; this approach assumes that the variances about the means are the same (Sutherst et al. 2000). Most important, no current climate-matching model fully incorporates the extent to which the climate at any site varies randomly in observed range extremes.

CLIMEX illustrates an approach that can narrow the estimate of the potential range of an introduced species or predict potential ranges from which a persistent nonindigenous species might emerge. Such models yield, in effect, a first evaluation or screening of potential range. Even if a species' native range appears to have a climate similar to a climate in the United States, the similarity by no means ensures that if it arrives, it will persist, much less that it will become invasive. Evaluation based particularly on the biotic component of a potential target range is also needed. Nevertheless, climate-matching deserves support and further evaluation (Kriticos and Randall 2001).

PREDICTION BASED ON TRAITS

Recurrence of some species as invaders in widely separated parts of the globe has long prompted the hypothesis that some species possess traits or attributes that enhance the probability that they will flourish in a new range. The hypothesis has been evaluated by searching for associations of life-history traits among these "repeat offenders" (mostly plants, but see Ehrlich 1989). For example, traits associated with known invasive pathogens include a short latent period, a long infectious period, a high rate of spore or propagule production, a high spore or propagule survival rate within and between growing seasons, efficient long-distance dispersal of spores, a wide host range, and environmental plasticity (Campbell and Madden 1990; van den Bosch et al. 1999). Examples of such pathogens with short latent periods and high rates of spore production are *Phytophthora infestans*, the cause of potato late blight, and *Puccinia graminis*, the cause of stem rust in wheat. *P. graminis* and *Phakopsora pachyrhizi*, the cause of soybean rust, are examples of pathogens with very efficient long-distance dispersal of spores. An invasive pathogen with a wide host range is plum pox virus (PPV). *Synchytrium endobioticum*, the cause of potato wart, is an example of a pathogen with very long survival times in the soil in the absence of a host plant. It is not known, however, if such information might be used to prospectively evaluate pathogens that are newly identified or not widespread.

As early as 1879 Henslow observed that many widespread British plants were self-pollinating and associated this trait with their independence from animal pollinators. Firm scientific foundations for work on the traits of invading plant species can be traced to Salisbury's long-term studies on the ecology of weeds in Britain (Salisbury 1961). Attention to this issue received a major boost with publication of the highly influential symposium volume *The Genetics of Colonizing Species*, edited by Baker and Stebbins (1965). Contributors to that volume provided much insight in identifying ecological and genetic characteristics most commonly found in invading species.

Baker (1965, 1974) compiled a list of traits found in the "ideal weed" (which is roughly analogous to the plant invaders dealt with here), including rapid development to reproductive maturity, high reproductive capacity, small and easily dispersed seeds, broad environmental tolerance, and high phenotypic plasticity. As Mack (1996b) has pointed out, the potential value of such characteristics to an invader are readily perceived, and many of the world's plant invaders do indeed possess some of them (reviewed in Brown and Marshall 1986). However, many species with no record of producing an invasion also possess many of the traits listed by Baker. In addition, the failure of surveys among floras to find support for "ideal weed" characteristics among invaders have led to challenges to the strength of earlier generalizations about the traits associated with plant invaders (Noble 1989, Perrins et al 1992a,b, Williamson 1996). Weeds that are invasive but have none of the traits attributed to invasiveness include *Watsonia bulbillifera* (wild watsonia) and *Homeria miniata* (two-leaf cape tulip) in Australia (Parsons and Cuthbertson 1992) and *Gunnera tinctoria* in Ireland (Clement and Foster 1994). Baker's list was also heavily biased toward traits commonly found in weeds of agricultural and ruderal habitats. Those habitats make up only a portion of the diverse environments invaded by plants; not surprisingly, diverse colonizing strategies are associated with invaders.

The shortcomings of attempts to use traits as a predictive tool have fueled skepticism about whether it would ever be possible to predict successfully which species would become invaders (Crawley 1987, Williamson and Fitter 1996). Traits commonly found among invaders are often assumed to contribute to these species' invasions, although this assumption is rarely demonstrated by appropriate ecological and demographic studies (Schierenbeck et al. 1994, Rejmanek and Richardson 1996). The design of such investigations is formidable because isolating features of an organism's life history that contribute substantially to fitness is difficult. Ideally, an investigator would be able to specify the combination of traits that cause invasiveness. However, evolutionary divergence is often so great that most life-history traits differ to some extent among even related taxa, and this divergence makes inferences difficult about the key features responsible for invasiveness. The less closely related the taxa, the more acute the problem becomes; however, even species comparisons involving congeners often reveal large differences in ecology and life history.

The difficulties of making predictions among broad taxonomic groups were recently demonstrated by Goodwin et al. (1999). They examined predictive capability on the basis of three plant traits related putatively to invasiveness: life form (annual or perennial), stem height, and flowering period. They then compared invasive and noninvasive European plant species in their new range in New

Brunswick, Canada. Two of the traits—height and flowering period—were significant components of a predictive model, but the model's predictions were no better than random. A second analysis that was based on the same variables as the first plus geographic range produced a model that contained only geographic range. This model produced predictions decidedly better than random, but the results nevertheless are disheartening: the species that are most likely to be transported to a new environment are also the ones most likely to become invasive because of their wider environmental tolerances.

Difficulties in prediction arise because organisms depend not only on individual characteristics, but also on interactions with their environment. That perspective is explicitly recognized in the familiar interaction term: genotype X environment = phenotype (Falconer 1981). The phenotype expressed in a particular environment governs the fitness of a genotype (Heywood and Levin 1984, Bradshaw 1984). Different environments elicit different phenotypic responses from the same genotype. By analogy, species responses vary among environments, so invasive potential depends on the environmental circumstances that an introduced genotype confronts. The importance of the environment is generally recognized in ecology and animal behavior, where there are numerous demonstrations of so called "context-dependent" responses of organisms to various ecological conditions (Heywood and Levin 1984, Sultan 1987). Thus, simply identifying the traits of a species and ignoring the environmental context in which the species occurs limits the information about whether the species can persist, let alone become invasive. Many species fail to display traits usually associated with invasive potential—high reproductive performance, wide geographic range, and so on—in their native ranges but behave differently in novel ecological settings. The contrast in responses between native and introduced populations arises without necessarily involving changes in life-history traits. That outcome is strong evidence of the importance of environmental context in predicting whether an introduced species will become invasive.

Assessing the outcome of "species X environment" interactions in terms of invasive potential is considerably more difficult than identifying traits displayed by a known invader. It requires knowledge of the range of environments that potential invaders are likely to encounter in their adopted homes and experimentation as to the species' responses to the new environments. Experiments are time-consuming, and simulating environmental variation is a formidable task, especially in an environmental growth chamber or experimental garden (Patterson et al. 1979, 1980, 1982). To predict invasiveness accurately, the experimenter would study potential invaders in an array of environments (Prince and Carter 1985, Mack 1996b). That approach entails risk: the experimental introductions themselves could escape, thereby sparking invasions.

Despite those difficulties, trait-based approaches hold appeal as a means of providing a general guideline regarding invasive potential (Reichard and Hamilton 1997). However, the predictive power of the approaches is directly proportional to the amount of ecological information available on attributes of an organism and a receiving environment. Trait-based approaches require an appreciation that the life histories of organisms are molded by evolution, which results in the "optimization" of fitness for a variety of environments. Individual traits rarely operate in isolation but are instead parts of life-history syndromes that represent an integration of traits in response to environment over time. Thus, an immigrant becomes an invader because it has adaptive suites of morphological, physiological, and ecological traits that arise and are conserved during the course of evolution.

The phylogenetic distribution of invaders may not be random among the earth's biotas. For example, among flowering-plant families, naturalized and invasive species, particularly those deemed weeds in agriculture, are more commonly represented among dicotyledonous than among monocotyledonous families (Parsons and Cuthbertson 1992). Indeed, it is probably the general observation that some groups appear more frequently than others on the lists of naturalized species that has motivated the search for traits associated with invasiveness. The search continues despite the recognition that diverse ecological strategies are associated with species' becoming invasive.

One way in which the identity of traits relevant to invasiveness has long been pursued is to survey large numbers of invasive species for taxonomic patterns. For example, Heywood (1989) concluded that most agricultural weeds come from the large families Asteraceae and Poaceae. Heywood (1989) and Cronk and Fuller (1995) identified these families and Fabaceae as containing many species that are invaders of natural areas. However, as pointed out by Daehler (1998), such surveys do not establish whether the number of invaders is higher in specific families than might be expected by chance alone.

Surveys of the above type, as in much ecological research, can reveal useful information, but they generally do not consider the phylogenetic relationships of taxa. Invaders rarely constitute a random sample of species or traits, so attempts to search for the correlated evolution of traits associated with invasiveness can suffer from phylogenetic nonindependence in that species are used as independent data points. Nonindependence tends to inflate degrees of freedom and increases the likelihood of type I errors (that incorrectly identify positive associations) in investigations searching for associations between traits and invasiveness. Recently, Crawley et al. (1996) used phylogenetically independent contrasts (PICs) and a molecular phylogeny of angiosperms to investigate ecological traits that distinguish native and introduced plant species in Britain. They found that introduced plants were taller, had larger seeds, were more likely to flower early or later in the flowering season, and were more likely to be insect-pollinated than their native counterparts. A lively debate has developed over the pros and cons of using PICs for addressing ecological questions (Harvey et al. 1996, Westoby et al. 1995); the availability of new phylogenetic data will aid in determining which traits are functionally associated with invasiveness.

Ideally, if invasiveness were found to have originated on multiple occasions within a phylogeny, it would be possible to determine whether particular traits are associated with the change in ecological behavior. Recurrent patterns among different lineages would help to identify key traits that initiate the evolution of invasiveness.

On the basis of a multivariate approach, results of several studies suggest that traits of invaders can, at least in some cases, be predicted (see Reichard and Hamilton 1997, Rejmanek and Richardson 1996). For example, Rejmanek and Richardson (1996) were able to predict the invasiveness of pines (*Pinus*) on the basis of a few simple biological traits. A discriminant analysis of 10 life-history traits in 24 cultivated pines species, half of which were considered invasive, demonstrated that seed mass, minimal juvenile period, and the interval between large seed crops were all closely associated with invasiveness.

What accounts for the abovementioned apparent success in predicting invasiveness? Most earlier work on traits associated with invasiveness involved large-scale surveys in which many taxa that differed widely in phylogeny and ecology were represented. Many factors are confounding in such datasets and are likely to obscure relations between life-history traits and invasiveness, because invasiveness might arise for diverse reasons in large taxonomically heterogeneous samples. Rejmanek and Richardson (1996) restricted their analysis to one taxonomic group of woody plants, thus minimizing that problem.

Another limitation in the analysis of traits is the bias of immigration (Mack et al. 2000). Comparisons of invasive and noninvasive members of any taxon are severely handicapped by the happenstance that has led some species to be transported to new environments many times, while some of their relatives to have never been carried outside their native environments. We have no empirical basis for predicting the role of the latter group in new environments or which of their traits facilitate, deter, or play no role in their persistence there.

Although there is generally good understanding of the factors and processes that contribute to invasiveness, the component traits lose predictive power when applied to a taxonomically diverse array of species. Predictive systems have so far focused almost exclusively on plants, and the successful systems are restricted to relatively small taxonomic groups. There is no consensus as to whether the current predictive systems for plants are sufficiently accurate or applicable in a comprehensive manner (Mack et al. 2000).

A SCIENTIFIC BASIS FOR PREDICTION?

Although neither a species' past performance in new environments nor its assemblage of traits is an adequate guide to forming comprehensive predictions on a species' invasive potential, these tools have value. The key question is whether there is a scientific means to improve on those tools for species that have no immigration history.

The considerable fundamental knowledge about the factors and processes that drive biological invasions should enable the fundamental structure of a predictive system to be described. The committee strove to identify those factors and processes evident in the science-based literature on invaders—hereafter referred to as "characteristics"—that could be used to predict invasiveness. It was not assumed that a functional predictive system could be developed now; rather, the committee considered whether it was possible to develop such a system at all. The framework that we developed can be considered a testable hypothesis that, if to used as a predictive system, must be empirically evaluated. From the outset, the committee determined that the characteristics must reflect the interactions of species traits (genotype) with environmental factors and that environmental factors would be both natural and human-mediated. The initial question asked was, "What general characteristics are indicative of or associated with organisms that arrive, persist, and eventually invade in new environments?" Groups of committee members worked independently to identify such characteristics for the major taxa considered (arthropods, plants, and plant pathogens) and then attempted to delineate how to quantify these characteristics and how the quantifications would be used to determine a likelihood for each of the stages of an invasion.

The committee identified combinations of species traits, environmental factors, and their interactions for organisms that were most likely to arrive at a foreign destination, persist, and invade. There was near unanimity of characteristics associated with arrival among the three taxonomic groups (Table 6-1a). For example, historical evidence of introduction elsewhere, high rate of movement from a source to a specific destination, high survival during transit, and escape from regulatory safeguards were viewed as common characteristics of nonindigenous species that were likely to arrive at new destinations. The ability to identify the characteristics that serve as predictors declined for the other two stages of the invasion process; this difficulty reflects the fact that the processes of arrival are strongly influenced by human activities and are reasonably well known, whereas the processes of persistence and invasion are often highly idiosyncratic. (Tables 6-1b and 6-1c).

Having identified characteristics thought to be useful for predicting the likelihood of each of the three stages of the invasion process, the committee asked how we might know, measure, or assign parameters to these characteristics. For example, a history of long-distance movement was identified as key information for predicting the arrival of a nonindigenous species. The logic here is straightforward: if the organism has been intercepted repeatedly, there is a high likelihood that it will arrive again. Thus, measuring the history of long-distance movement could be as simple as "yes" or "no" and based on historical records. Three other categories of information were also identified as likely predictors of arrival: the rate of movement from a source to a potential destination, survival during transit, and escape from safeguards (such as inspection or control mea-

TABLE 6-1a. Characteristics of Nonindigenous Pathogens, Plants, and Arthropods Thought to be Indicative of Likelihood of *Arrival* in New Habitat or Range and Information Needed to Functionalize the Characteristics

	Information Needed		
Characteristic	Pathogen	Plant	Arthropod
History	• Is there historical (archival) evidence of repeated introduction of the pathogen?	• Has the plant been frequently and recently intercepted outside its native range?	• Has the arthropod been frequently and recently intercepted or detected in North America?
Rate of movement from source to potential destination	• Is the pathogen commonly associated with the import (commodity, plant, or conveyance) in or coming from the country of origin? • Is the volume of the imported material great? • Does the pathogen have a wide geographic range? • Can it be moved passively (airborne or birds)?	• Does the taxon have a wide geographic range? • Does the plant occur in a wide array of environments? • Does the plant have demonstrated or alleged human value? • Are the frequency and volume of trade between the plant's existing range and its potential new introduction point high?	• Does the arthropod have a strong association with the imported product? • Is the volume of imported material large? • Does the arthropod have a wide geographic range (proportional to likelihood of transport)? • Does the arthropod, at some times, have high population densities in its native range?
Survival during movement	• Can the pathogen survive transit?	• Does the plant have a durable resting stage (seeds or vegetative structures)?	• Is the arthropod likely to survive transport?
Escape from safeguards	• Can the pathogen be detected, and is there a recognized detection or mitigation procedure either at the point of origin or at the destination?	(Information for plants is inadequate)	• Can the arthropod be detected, and is there a recognized procedure for detection or mitigation either at the point of origin or at the destination?

TABLE 6-1b. Characteristics of Nonindigenous Pathogens, Plants, and Arthropods Thought to be Indicative of Likelihood of *Establishment* in New Habitat or Range and Information Needed to Functionalize the Characteristics

	Information Needed		
Characteristic	Pathogen	Plant	Arthropod
History		• Is there a history of naturalization?	• Is there a history of establishment in a similar environment elsewhere outside its native range?
Environment suitability	• Is there a similarity in the physical habitat between the point(s) of origin or other naturalized range of the pathogen and potential destinations?	• Is climate similar between the current geographic range and potential destinations?	• Is climate similar between the current geographic range and potential destinations?
Resources-host-habitat finding	• Is a suitable (susceptible) host that can maintain a base level of pathogen reproduction present? • Are potential hosts in spatial and temporal synchrony with the pathogen? • Does dissemination depend on a vector, and, if so, is the vector present? • Is the pathogen excessively virulent?	(Not considered a major restrictor for plants)	• Are potential hosts spatially and temporally available to the arthropod? • Is there biotic resistance, mostly in the form of natural enemies that would limit survival?
Overcoming demographic and environmental stochasticity	• Does the pathogen have a means of surviving adverse habitat or environmental conditions? • Is the inoculum pressure high (multiple foci, large population, or large number of propagules)?	• Is the propagule pressure (number of founders, frequency of introductions, or spatial distribution) high? • Is the time to first reproduction short? • Does the plant have a dormant period? • Is there uniparental reproduction?	• Is the propagule pressure (number of colonists, possible introductions per year, and possible locations) high? • Is there uniparental reproduction? • Does the arthropod have a high growth rate?

TABLE 6-1c. Characteristics of Nonindigenous Pathogens, Plants, and Arthropods Thought to be Indicative of Likelihood of *Invasion* in New Habitat or Range and Information Needed to Functionalize the Characteristics.[a]

	Information Needed		
Characteristic	Pathogen	Plant	Arthropod
History	• Is there a history of the pathogen causing detrimental effects to plants elsewhere?	• Is there a history of invasiveness elsewhere?	• Is there a history of thriving elsewhere outside native range?
Host-habitat availability	• Is the host range wide? • Are susceptible hosts widespread? • Has the pathogen demonstrated diversity in pathogenic traits?	• Does the plant occur with disturbance or in cultivation?	• Are potential hosts contiguously distributed?
Dispersal	• Does the pathogen have means of rapid and widespread dispersal?	• Does the plant have a means of rapid and efficient dispersal? • Does the plant possess a fleshy fruit?	• Does the arthropod have an effective means of dispersal (natural or human-assisted)?
Growth	• Does the pathogen have a high reproductive capacity?	• Does the plant have a high reproductive output through seeds or asexual propagules? • Is the plant closely related to native flora?	• Is there biotic resistance that will limit growth?

[a] Note that species must persist (Table 6-1b) before invasion can occur.

sures). For each of those characteristics, information that would be required to assign parameters to the characteristic was identified. For example, to assign parameters to an insect's movement from a source to a potential destination, the committee thought it important to know whether the insect has a strong association with an imported material, whether it has a broad geographic host range, whether it has high densities periodically in its native range, and the volume of imported material with which it is associated. That information is important because immigration via an imported material will be a function of the infestation rate and the quantity of the material or product being imported. Infestation rate will depend in part on the insect's density in its native range, and density is often associated with geographic range. Furthermore, the likelihood that the species will be transported appears to be related to the size of its geographic range (Ehrlich 1989), which could be related to the likelihood of being inadvertently included in exported cargo.

Identification of the requisite information and data was more difficult for the persistence and invasion stages (Tables 6-1b and 6-1c). More important, it was not clear how to use the information and to assign parameters. In fact, it was rarely clear on what scale the parameters should even be arrayed. For example, even if information on rate of movement were available, we could not identify how it should be arranged to provide a unit that described movement, or even whether it should be "yes" or "no"; "high", "medium" or "low"; or some number in the interval 1-10. This dilemma was encountered for each of the characteristics identified.

Another example reinforces the point mentioned above. An essential characteristic leading to the survival of a newly arrived nonindigenous species is the ability to overcome demographic and environmental stochasticity (see Chapters 3 and 4). For plants, the needed data include whether the propagule pressure is high, whether the time to first reproduction is short, whether the plant has a dormant period, and whether there is uniparental reproduction. Answering those questions leads immediately to further questions: When is propagule pressure high? What is a short time to first reproduction compared with a long time or an intermediate time? How long need the dormant period be, and when must it occur? Even if the primary questions were answered and answers to the secondary questions were available, it is not clear how answers to the primary questions would be used to obtain a way to account for demographic and environmental stochasticity. In fact, it is not obvious what this accounting should be: should it be dichotomous, categorical, or continuous?

The dilemma faced in using a predictive system for invasiveness is summarized in Figure 6-1. Characteristics of nonindigenous organisms that could contribute to invasiveness and characteristics of the environments into which they are introduced are reasonably well known. Less well understood are the types of data needed to quantify these characteristics. Poorly known is how to assign parameters to the characteristics and how the parameters are to be used in algorithms to determine the likelihood of each stage of the invasion process. Even if those limitations are surmounted, much of the needed information is usually unavailable for species that might be introduced. The lack of data not only prevents the framework from being used, but also keeps the level of uncertainty in the framework from being estimated.

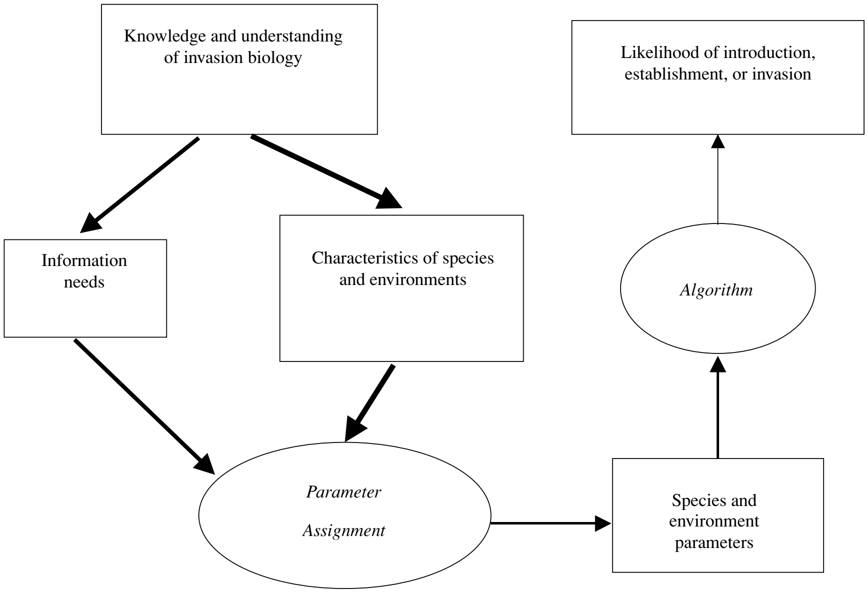


FIGURE 6-1 General structure of system for predicting invasiveness of nonindigenous species. Knowledge and understanding of invasion biology allow identification of the genotypic and environmental characteristics of invasive species and of information required to assign parameters to these characteristics. Parameters are then used in algorithm to estimate likelihood of stages of invasion. Ellipses represent processes in system; boxes state variables. Width of arrows represent levels of certainty in process; thicker arrow mean higher levels of confidence.

Although not the entire answer to the problems raised above, the results of deliberate experimentation would contribute substantially to their solution. For example, controlled experimental field screening for potentially invasive species could be pursued for plant species whose features are associated with establishment and rapid spread without cultivation and whose immigration history is unknown. In addition to averting the release of a potentially invasive species, results of field trials would substantially enhance the ability to detect common patterns of plant performance in new environments. Similar efforts to acquire life history and population level data in situations that approximate field settings would be beneficial for predicting the fate of nonindigenous arthropods and pathogens that are of concern, including species proposed for deliberate introduction. The logistical difficulties and costs of implementing such studies are likely to be greater for arthropods and pathogens than for plants, but extending this approach to arthropods and pathogens would similarly provide valuable information about the capacity of these organisms for population growth and spread and improve the ability to predict invasiveness.

Quantifying a species' performance in environments it has not before encountered can only be accomplished through experimentation (Hairston 1989, Mack 1996a). Our inadequate knowledge of the early stages in an invasion demonstrates the need for experimentation based on carefully constructed hypotheses about a species in specific ranges under measured environmental conditions. For example, detailed demographic information among populations and cohorts occurring in different environments is essential if we are to predict the outcome of these critical periods in the course of an invasion (such as Mack and Pyke 1983, 1984; Grevstad 1999a,b). Such a protocol already exists in the USDA Agricultural Research Service plant germplasm introduction and testing laboratories. These laboratories evaluate new accessions, including pasture and range species, for their likelihood to contribute to U.S. agriculture. Their goal is to identify species that will grow profitably in the United States—that is, free of predators, pathogens and competitors (USDA 1984). Species deemed free of such hazards should however be reviewed carefully before release because many features that are prized in land reclamation, rangeland management and landscape horticulture are the same features that could enhance these species' persistence outside cultivation in the United States (McArthur et al. 1990). A geographically broad network of experimental gardens to identify species that could readily spread and persist upon release should be established**.** Extending these ideas to arthropods and pathogens, including those under consideration for deliberate introduction, would be valuable, although practical considerations associated with experiments in field settings may be more difficult to overcome. Well-designed studies that obtain information on life history traits, interactions with native species and population level parameters in a realistic environmental context could provide valuable information about the potential for population growth and spread of an arthropod or pathogen in a new habitat, and increase our overall understanding and ability to predict invasiveness.

RISK ASSESSMENT

From our discussion thus far, it is clear that we do not have a comprehensive taxonomically based ability to predict with sufficiently high accuracy whether, when, or how a nonindigenous species will become established in a new range. Others have reached the same conclusion (Mack et al. 2000, Williamson 1996). However, our knowledge of the factors and processes that mediate invasion can be used in a related endeavor: risk assessment. Risk assessment can provide valuable insights into both the likelihood of an invasion and its consequences, and these insights can prove useful for forming management strategies and policies.

Risk is the product of the likelihood of an event or process and its consequences As a result of the joint consideration of likelihood and outcomes, events with low to moderate likelihood but serious consequences can carry high risk, whereas events with high likelihood but insignificant consequences often carry little, if any, risk. Although predicting the likelihood of invasion by nonindigenous species has much appeal, from a practical perspective it is risk that must be evaluated. Risk incorporates the economic and environmental outcomes of invasions, and these outcomes are of primary importance to society.

Further rationalization for engaging in risk assessment rather than prediction of invasiveness itself arises from the uncertainty that will accompany most predictions of invasiveness compared with assessments of risk. Uncertainty refers to the degree of confidence in a prediction or assessment (Kammen and Hassenzahl 1999). If only the likelihood of a nonindigenous species' becoming established in a new environment is considered, it is difficult to apply the level of uncertainty in this prediction fully in decision-making. But if the consequences of an invasion are considered, uncertainty can be incorporated into the evaluation of risk. Greater caution might be used in response to the uncertainty about events and processes that can have serious consequences. Thus, with respect to the practical application of predicting biological invasions, it is the risk posed by invasion by a particular species that should be evaluated.

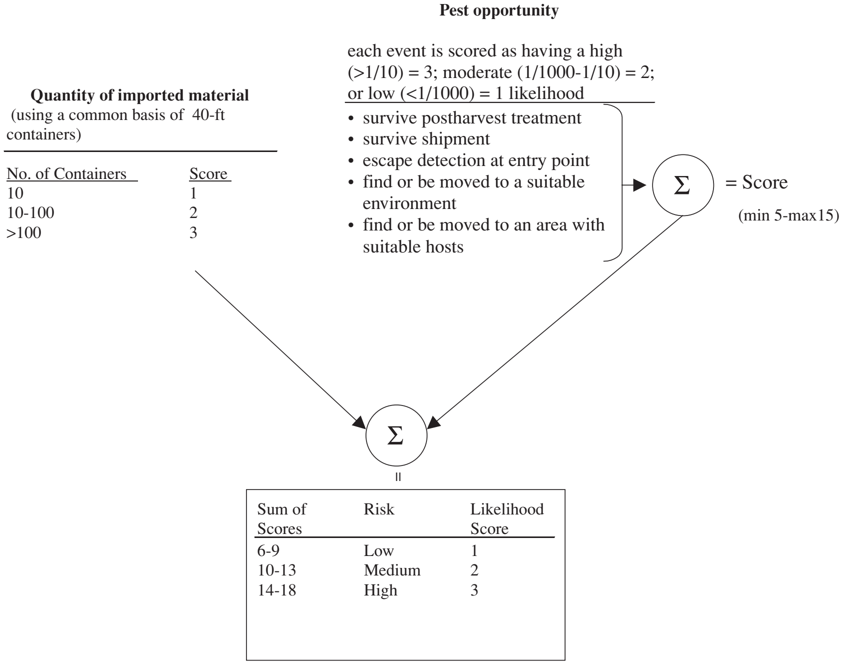
Several systems have been devised for evaluating the likelihood that a nonindigenous species will become invasive, and they all share a qualitative structure. They assess the likelihood that a nonindigenous species will arrive, become established, and proliferate and spread with a set of species traits and environmental characteristics. In that regard, they are similar to the predictive structure shown in Figure 6-1. Usually, the characteristics are described in a dichotomous fashion (for example, present or absent), and the likelihood measures are categorical (for example, high, medium, or low). The systems also rely on the qualitative assessment of consequences, usually by indicating whether consequences will occur. A collective measure of consequences is determined by summing the expected occurrences of individual consequences (such as crop loss, decreased market, or direct impact on endangered species). The estimate of likelihood of establishment and expectation of consequences are combined to identify a categorical estimate of risk.

Two specific pest risk-assessment procedures are portrayed in Figures 6-2 and 6-3. Figure 6-2 depicts a generic system used by the Animal and Plant Health Inspection Service (USDA/APHIS 1997). The likelihood of pest introduction is based on the estimated quantity of imported material and "pest opportunity", which is a synthesis of the arrival and establishment stages of the invasion process. It is somewhat incongruous that pest opportunity is measured as a sum of scores that have a probabilistic basis. Because these scores represent subjectively determined probabilities, their joint consideration should reflect the multiplication of the chains of independent probabilities to determine their joint likelihoods. The

A. Pest Risk Potential

Consequences of introduction score + Likelihood of introduction score	Pest risk potential rating
2	Low
3-4	Medium
5-6	High

B. Likelihood of Introduction



Quantity of imported material
(using a common basis of 40-ft containers)

No. of Containers	Score
10	1
10-100	2
>100	3

Pest opportunity

each event is scored as having a high (>1/10) = 3; moderate (1/1000-1/10) = 2; or low (<1/1000) = 1 likelihood

- survive postharvest treatment
- survive shipment
- escape detection at entry point
- find or be moved to a suitable environment
- find or be moved to an area with suitable hosts

Sum of Scores	Risk	Likelihood Score
6-9	Low	1
10-13	Medium	2
14-18	High	3

FIGURE 6-2 Qualitative pest risk-assessment procedure used by USDA/APHIS (1997). Risk potential (A) is based on joint consideration (addition) of likelihood of introduction and consequences of introduction. Likelihood of introduction (B) is based on quantity of imported material and qualitative assessment of the likelihood that nonindigenous species will survive or find suitable host or habitat. Consequences of introduction (C) are based on qualitative assessments of climate-matching, pest host range and dispersal, and economic and environmental impacts.

C. Consequences of Introduction

1) Climate-host interaction
no. of U.S plant hardiness zones with suitable climate and hosts

Zones	Score
>4	High - 3
2 or 3	Medium - 2
1	Low - 1

2) Host range
risk assumed to be correlated with host range

Host Range	Score
• multiple species in multiple families	High - 3
• multiple species in one family	Medium - 2
• one or more species in one genus	Low - 1

3) Dispersal potential

Characteristics	Score
• high reproductive potential *and* capable of rapid dispersal	High - 3
• high reproductive potential *or* capable of rapid dispersal	Medium - 2
• neither of the above	Low - 1

4) Economic impact

- lower yield in a host crop
- lower value of the commodity due to increased costs, lower market value, or both
- loss of markets due to new quarantines

no. of impacts	Score
all 3	High - 3
2	Medium - 2
1	Low - 1

5) Environmental impact

- significant direct environmental impacts
- direct impacts on endangered or threatened species
- indirect impacts on endangered or threatened species
- lead to control measures, including use of toxic chemicals
- lead to biological control with nonindigenous organisms

No. of impacts	Score
>2	High - 3
1	Medium - 2
none	Low - 1

CONSEQUENCES OF INTRODUCTION
equal to cumulative score of risk elements 1-5

Cumulative Score	Risk Rating	Risk Score
5 – 7	Low	1
8 – 11	Medium	2
12 – 15	High	3

FIGURE 6-2 Continued

consequences of introduction are determined as the sum of scores for five “risk elements”. Three risk elements refer to the invasion process, and two refer to the consequences of invasion. Thus, in this system, consequences are assessed as a composite measure of the spread and abundance of a newly introduced species and impacts that stem from the invasion. On the basis of the characteristics listed in Table 6-1, it is questionable whether the three risk elements that putatively capture the likelihood of invasion by an introduced organism are reliable. The overall pest risk does, however, reflect the combined influences of likelihood and consequences of introduction.

The second pest risk-assessment protocol (Figure 6-3) has been proposed for use with solid-wood packing materials (USDA/APHIS-FS 2000). This system more clearly delineates the invasion process (likelihood of introduction) and its consequences. It also models the process for determining the likelihood of introduction as akin to a set of independent events that must all occur for the immi-

A. Pest Risk Potential

Likelihood of introduction [a]	Consequences of introduction [a]		
	H	M	L
H	H	H	M
M	H	M	M
L	M or L[b]	M or L[b]	L

[a] H = high, M = moderate, L = low

[b] If two or more elements that determine likelihood of introduction are low, pest risk potential is low.

FIGURE 6-3 Qualitative pest risk-assessment procedure proposed for use with imported solid-wood packing materials (USDA 2000). Pest risk potential (A) is based on qualitative assessment of likelihood of pest introduction (B) and consequences of introduction (C). Likelihood of introduction (B) is based on series of processes and is similar to result of multiplying probabilities of independent events to obtain joint probability. Likelihood of each process (such as association with commodity at point of origin or entry potential) is assigned score of high, medium, or low on basis of whether one or more criteria are deemed true. For example, entry potential is considered high if there is history of repeated interceptions or if two of followng three criteria are true: one or more life stages of pest likely to survive transport, pest not likely to be separated from host, and pest is difficult to detect. Consequences of introduction (C) are essentially sum of individual consequences, although consequences do not carry identical weights. Each consequence (such as, economic damage potential) is assigned score of high, moderate, or low on the basis of whether one or more criteria are true. Pest risk potential is based on joint consideration of likelihood of introduction and consequences of introduction.

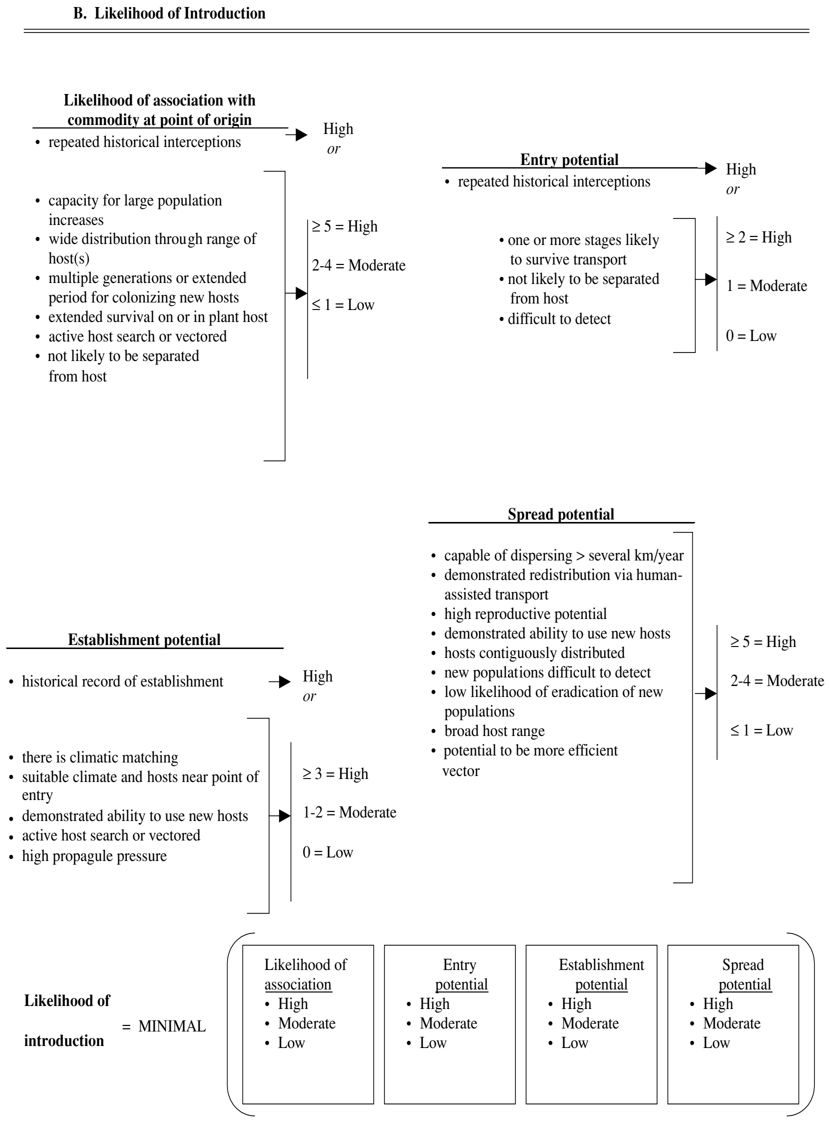


FIGURE 6-3 Continued

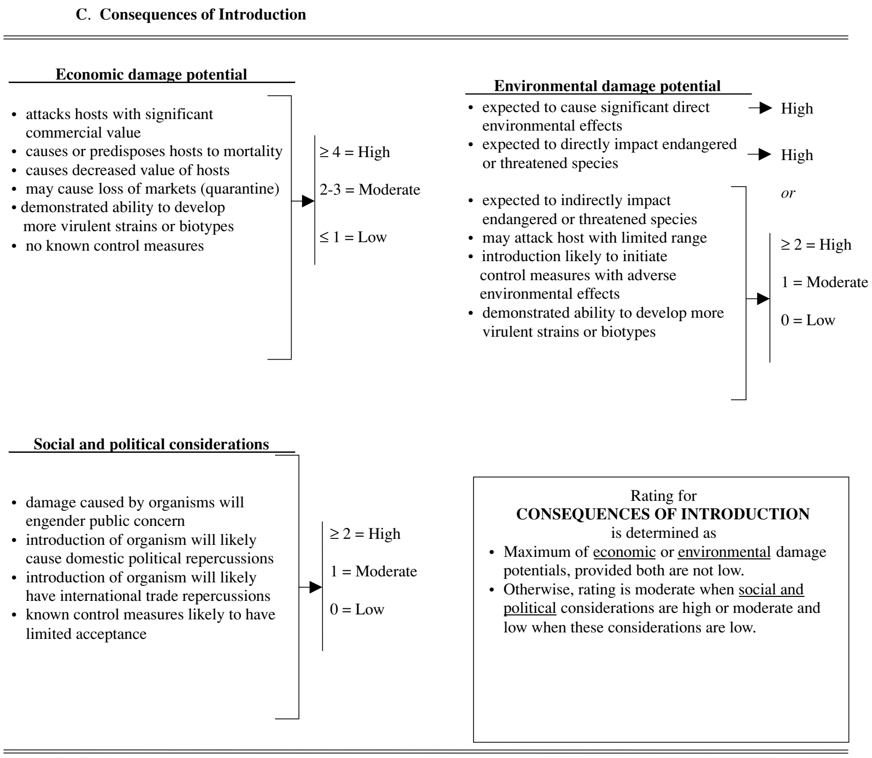


FIGURE 6-3 Continued

grant population to develop an invasive population (that is, the multiplication of probabilities). As with the first system, the overall risk reflects the combined influences of the likelihood of introduction and consequences of introduction.

Because risk-assessment systems use the same structure as that depicted in Figure 6-1 to assess the likelihood of introduction, they share the limitations identified for a scientifically based prediction of invasion. Foremost among the limitations is that risk-assessment systems require subjective determination of characteristics of nonindigenous species and the environments into which they might be introduced, and they identify the risk of introduction by subjectively placing species and environmental characteristics into likelihood categories. If the characteristics for assessing the likelihood of introduction shown in Figure 6-3 are used as an example, it is not clear how one would determine whether an organism has a high capacity for increase, what the capacity is for dispersing, or what constitutes an extended period for colonizing new hosts. Those determinations are made subjectively and are thus susceptible to bias. Furthermore, none of the mapping systems used to identify likelihood of introduction based on those characteristics has been fully validated. Even validation of the Australian weed risk-assessment system (see Box 6-1) can be viewed as somewhat equivocal. Thus, these components of current pest risk-assessment systems cannot yet satisfy the science-based criteria of repeatability and peer review for validity. Simberloff and Alexander (1998) came to similar conclusions when they reviewed risk-assessment systems.

Similar criticisms can be leveled against the procedures by which the component of the risk-assessment systems dealing with consequences are assembled. Much of the information required to assess consequences is based on expert judgment, which is often subjective, can vary substantially among evaluators, and can be influenced by political or other external factors. To our knowledge, the algorithms used to categorize the overall consequences have not been validated. Furthermore, uncertainty is never explicitly incorporated into the evaluation process. In some cases (such as in the International Plant Protection Convention protocol), uncertainty is recorded but apparently then ignored.

Pest risk-assessment systems have value, provided that the reasoning used is underlain by careful documentation. The process of conducting a qualitative risk assessment is at least as valuable as the specific risk values that are produced, because the process, when carefully documented, provides a mechanism for assembling and synthesizing relevant information and knowledge. Furthermore, the process of risk assessment catalyzes a thorough consideration of the relevant events. When a consistent and logical presentation justifies the parameters used in a risk assessment and its conclusions, assessments can meet the scientific criteria of transparency and openness. Many risk assessments use slightly different characteristics and methods for determining likelihood, depending on the specifics of the situation being considered. That variability is a strength of the risk-assessment systems, not a shortcoming.

In the absence of careful documentation, specific risk values are worthless. That is a serious problem because any specific value imparts to some policy-makers and a large part of the public a scientific aura and a sense of knowledge that might not be warranted. Pest risk assessments that lack careful documentation can do more harm than if no assessment had been undertaken.

A recent risk assessment of the introduction of the cape tulip (*Homeria* spp.) (USDA/APHIS 1999) illustrates both the limitations and the strengths of qualitative risk assessment (see Box 6-2). Determination of the likelihood of introduction is the principal weak point in the assessment. The most apparent problem is the lack of rationale for the scores given in the pathway analysis. The analysis fails the test of transparency; there is little way to critique the scores other than to say that they are unsubstantiated. A weakness in the protocol used is that scores are summed rather than viewed as the likelihoods of events in a sequential chain. For grain imports and ornamental plant shipments, the risk assessment indicated only a low likelihood that *Homeria* will escape detection at the point of entry. If

BOX 6-1 Western Australia Weed Risk-Assessment System

Some states in Australia have established their own weed-assessment system in addition to using the federal system developed by the Australian Quarantine and Inspection Service (AQIS). The system for Western Australia (WA) is perhaps the most elaborate of these state systems (Randall and Stuart 2000). In establishing their own systems, states in Australia have recognized that environments at one end of the Australian continent differ enormously from those elsewhere in the country, and a nonindigenous species could well be invasive in one state or region and be innocuous (or even fail to become established) in another.

The WA system was designed primarily to evaluate requests for the deliberate introduction of plants into the state, but its protocol could also be applied to accidental introductions. Unlike the AQIS system, the system for WA is not trait-based but relies extensively on the history of nonindigenous species in WA and elsewhere. Expert judgment (for example, "assessors decision points") is used to determine the extent to which a species with a history of naturalization might pose a threat in WA. An essential component of the system is the large database of species and their ecology that has been compiled by R. Randall, plant profiler, for Western Australia Agriculture. In addition, the protocol uses the results from a climate-matching program (CLIMEX) in determining whether the species could persist anywhere in the state, on the basis of the similarity of climates in the native range and potential new ranges in WA. Although the system appears to operate as a basis of allowing or prohibiting any proposed species entry, a risk assessment is performed, in effect, through determination, with a full weed assessment, that a species is an important weed and poses an immediate or imminent threat.

The WA system includes an essential but often overlooked component of assessment—correct identification of the species. The assessment of nonindigenous species worldwide contains celebrated cases in which evaluation and control were delayed by the misidentification of species that proved harmful. For plants

that is true, the overall likelihood of introduction should also be low. The analysis of consequences is more robust, and justification, including relevant literature, is provided for each of the rankings. Furthermore, although the characteristics used to determine the likelihood of invading (as part of the consequences evaluation) might be challenged, it is clear what characters were used and how they were determined.

Quantitative scenario analysis (Kaplan 1993, Firko 1995a) has been used to produce quantitative assessments for the likelihood of establishment. The process involves identifying and enumerating all potential pathways by which establishment can occur. Probability distributions are used to model the likelihood of each link in the chain and combined to estimate the overall likelihood of a nonindigenous species becoming established (Figure 6-4). Managing the risk consists that are being deliberately introduced, the correct identification cannot be entrusted totally to the applicant. The past performance of any congeners of the species is also considered in the evaluation. Having a congener with a record as a weed elsewhere does not automatically cause a species to be prohibited entry, but it does prompt further assessment. Use of records of congeneric weeds prompts further investigation at several points in the flow diagram.

An important feature of the WA system is that final approval of entry of a species is not usually automatic, especially for species for which there is no record. There are in effect several layers of examination and evaluation that each species must pass through before import approval is given. This multilayer system contains benefits for both the public and the applicant for species entry. Only a species that appears on a federal or WA prohibited list is automatically excluded from further evaluation. A species that is already naturalized in the state may be allowed entry (that is, entry of additional populations), although there is provision that these introductions may be denied. As a result, blocking their entry can reduce the amount of genetic variation in a species in the state. Although a record of a species as a "significant weed" (one demonstrated in the scientific literature to have an impact in agriculture or natural ecosystems) does not automatically prohibit a species from entry into the state, it does prompt a full weed assessment. Such assessments are more detailed examinations of the record of behavior of the species than simply whether it appears as a weed anywhere. A decision can be made after this assessment to prohibit or permit the species' entry. One apparent anomaly concerns the history of established domestic and international trade in the species; it is not clear to what degree a species with such a trade history would be permitted entry.

The strength of this system appears to depend on the comprehensiveness of the database maintained on nonindigenous species; that is, expert judgment here is based largely on known behavior of the species outside WA (Randall and Stuart 2000).

of reducing the likelihood of events in the chain. Although this method is quantitative, it often requires substantial subjectivity in assigning the probability distributions used to represent events along a pathway. Ideally, empirical data would be used to select the distributions, but such data are often not available.

As currently used, the method considers only the arrival and initial survival of a nonindigenous species, processes that usually are much better understood than the proliferation and spread phase of an invasion. Quantitative scenario analysis should be expanded to include all aspects of the invasion process, especially when consequences are high. The array of information suggested by the committee in Table 6-1 could be incorporated in scenario analysis to reflect a more comprehensive and realistic perspective on the risk posed by the introduction of pests and of organisms intended as biological control agents.

BOX 6-2 Summary of a Risk Assessment of Cape Tulip Introduction

Homeria, or cape tulip, of which there are 30-40 species, are native to South Africa and are widely propagated as ornamentals. An assessment was initiated by a request to import oats from Australia that might contain *Homeria* spp. In Australia, these species are weeds. They produce glycosides that are poisonous to livestock and humans. Potential impacts of cape tulips include livestock poisoning, reduced crop yield, changes in plant community structure, human poisoning, and increased use of herbicides to control the plants after their establishment. Species in this genus already occur in the United States outside cultivation.

The likelihood of establishment was assessed by identifying three potential pathways and assigning qualitative likelihoods to each of five events for each pathway. The likelihood of each event was judged to be low ($p < 0.01$), moderate ($0.01 \leq p \leq 0.1$), or high ($p > 0.1$), with numerical scores of 1, 3, and 5, respectively. The pathways, pathway events, and scores appear in Table 6-2. Note that this table is based on the risk elements for "pest opportunity" in Figure 6-2. Numerical scores for the likelihoods were summed, and the likelihood of establishment was determined by using the sum. If the sum of scores was 7-14, the likelihood of introduction was judged to be low (1); 15-24, moderate (2); and above 25, high (3). On the basis of a total of 63, the likelihood of establishment was judged to be high.

The consequences of establishment were based on the summation of four quantitative criteria, each of which was given a ranking of low, medium, or high (1, 2, or 3, respectively). The first criterion was the suitability of the habitat for widespread distribution. On the basis of relevant literature and predictions from CLIMEX (Sutherest et al., 1991a) this was rated high with a score of 3 (suitable climate would allow the weed to establish in four or more plant-hardiness zones). The second criterion was the ability to disperse and spread, which was also rated high, on the basis of the plants' having a high reproductive potential and highly mobile propagules. A checklist of characters thought to influence reproduction and dispersal was consulted to derive the rating. Characters contributing to dis-

An example of scenario analysis that takes a broad approach is a risk assessment of threats to a wetland system in Ottawa, Ontario, which included sorting out the nature and magnitude of several factors, only one of which was a nonindigenous plant (Foran and Ferenc 1999, Moore 1998). The scenario analysis broadly evaluated the ecosystem, the factors influencing the system, and the known, unknown, and expected responses of the system to stresses. By creating a matrix with all identifiable components in the stress (cause) and effect profile, the assessment was able to focus on the most relevant pathways and effects. The assessment concluded that the nonindigenous plant posed the greatest risk to the wetland system. This assessment intentionally included all parts of the sourcepersal and spread were prolific seed production; reproduction by corms; dispersal by wind, water, machinery, animals, and humans; and the ability of seeds and corms to tolerate some stress. The third criterion was an economic-impact rating that was based on potential reduced crop yield, lower commodity values, and possible loss of markets. The impact was rated as high on the basis of the potential economic loss from stock poisoning and reduced crop yield. The fourth criterion was environmental impact, which was also scored as high on the basis of potential impact on community structure and human health and the impact of control practices. The total score for the consequences assessment was 12, leading to an overall rating of high consequences (score of 3). The final measure of risk was based on the sum of the score for risk of establishment (3) and the score for consequences (3). That sum led to an overall evaluation of high risk.

TABLE 6-2 Pathways, Pathway Events, and Likelihood Scores for *Homeria* Risk Assessment.

Pathway	Event and Likelihood (1, 3, or 5)					
	Survive Treatment	Survive Transport	Escape Detection	Find Suitable Environment	Find Suitable Substrate	Total
Passenger baggage	5	5	3	3	5	21
Grain imports	5	5	1	5	5	21
Ornamental-plant shipment	5	5	1	5	5	21
Total						63

exposure pathway-response relationships and did not focus on only one part or one pathway.

The advantage of a scenario system is that it captures the ecological context, as recommended in present ecological risk assessment (Suter 1993, USEPA 1998). All the information is used, and a line of evidence is set aside only after compelling evidence warrants that action. The greatest limitations are that the analysis can be data-intensive and still remain blind to novel and unknown conditions. Modeling and use of related data can overcome some problems related to missing data, and peer review might be able to address some of the issues related to unknown conditions.

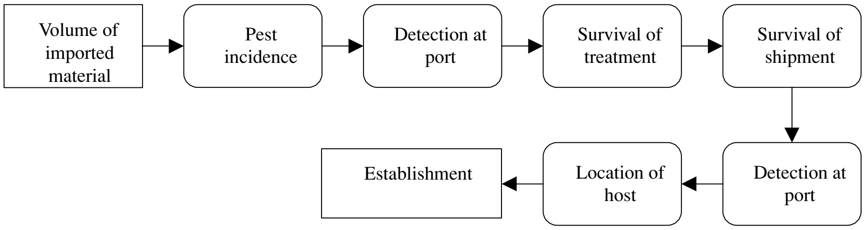


FIGURE 6-4 Generic pathway for quantitative scenario analysis. Rectangles are rates and rounded rectangles are probabilities. Analysis consists of describing probabilities using probability by distributions and parameterizing the volume(s). Monte Carlo simulation is used to estimate rate of establishment.

Pest risk assessment meets a crucial need in that it furnishes a framework for gathering and synthesizing information about a nonindigenous species and about the consequences of its becoming invasive. Those strengths have been recognized, and principles for conducting pest risk analyses have been outlined (Gray et al. 1998). We have discussed several of these principles, but three warrant recapitulation. First, because expert judgment must be used for estimating the characteristics and parameters used in pest risk assessments, the judgments must be clearly identified and supported. Second, the components in pest risk assessments must be completely documented, including the data that are considered and used; models, their assumptions, and results; and sources and justification of parameter values and other relevant facts. Third, pest risk assessments should be subject to peer review. Although risk assessment is not a scientific exercise, it is science-based and the most reliable method to evaluate its scientific credibility is peer review; such review should strengthen and refine analysis and not be viewed as an attack to be deflected.

KEY FINDINGS

- Predicting the invasion of introduced organisms in a new range has been based largely on identifying species that already have a record of invasiveness. Thus, the record of a plant's invasiveness is currently the most reliable predictor of its ability to establish and become invasive in the United States. The same is true for arthropods and pathogens if host plants on which they have colonized elsewhere exist in the United States.
- Climate-matching simulations can narrow the estimated potential range of an introduced species or estimate potential ranges from which invasive species might emerge. Such models form, in effect, a first evaluation or screening of a

species' potential new ranges. Even if a species' native range appears to have a climate similar to a climate in the United States, the similarity by no means ensures that if the species arrives it will persist, let alone become invasive. Evaluation based particularly on the biotic components of a potential target range is also needed, but it is difficult to incorporate this component into a simulation.

- Trait-based approaches for predicting invasiveness hold much appeal as a means of providing a general guideline regarding any species' invasive potential. However, the predictive power of these approaches is directly proportional to the amount of ecological information available on a species' attributes, the species' new environment, and the often stochastic circumstances surrounding its entry. The expression of species' attributes are context-specific (that is, environment-specific).
- The phylogenetic distribution of invaders is not random among the earth's biotas. However, evolutionary divergence is often so great that even closely related taxa can differ greatly in many life-history traits. That divergence makes it difficult to infer the key features responsible for invasiveness. The more distantly related the taxa, the more acute the problem; however, even species comparisons involving congeners often reveal large differences in ecology and life history. The availability of new detailed phylogenetic data will aid in determining which traits are functionally associated with invasiveness.
- Predictive systems have so far focused almost exclusively on plants, and the successful systems are restricted to relatively small taxonomic groups. There is no consensus as to whether the current predictive systems for plants are also conceptually appropriate for plant pests and for defining the risk posed by introducing organisms for biological control.
- There is considerable fundamental knowledge about the factors and processes that drive biological invasions, and a fundamental structure of a predictive system can be defined. Erection of comprehensive predictive systems is stymied, however, by the lack of adequate experimentally derived information on the behavior of species in different environments. Such information would place useful bounds on the functional elements in any predictive system.
- Until a comprehensive system for predicting invasion is developed, the uncertainty inherent in prediction can be evaluated most practically in the context of risk assessment. Its strength is that it incorporates the economic and environmental outcomes of invasions; these are the outcomes that are of primary importance to society. Risk assessments that are carefully documented and that explain the logic of their rating systems are more likely to result in repeatable conclusions in the hands of different experts. The committee advocates the creation of a comprehensive predictive system for identifying future invasive species based entirely on the interactions among a given species' biology, the environment it enters, and the circumstances of its residence in the new range. Risk assessment is an interim approach. Through its attention to species that may have substantial

environmental or economic consequences in a new range, risk assessment reduces dependence on the fundamental biological information needed in a purely predictive system. Species that are deemed to have a high risk of damage are highlighted even if the understanding of their biology is incomplete. Finally, risk assessments that are carefully documented and transparent in the logic used to assemble their ratings would allow public scrutiny and independent evaluation.

7

Enhancing the Science in a Science-Based System

CONCLUSIONS

Predicting the threats posed by nonindigenous plants, arthropods, and pathogens to plants in the United States is and will continue to be a substantial challenge. Having considered what is known about the development of invasions and about attempts to use that knowledge in a predictive manner, the committee reached the following four conclusions:

Conclusion 1. The record of a plant's invasiveness in other geographic areas is currently the most reliable predictor of its ability to establish and invade in the United States. The same is true for arthropods and pathogens if plants that they can use elsewhere occur in the United States.

Reliance on natural history, that is, empirical studies and careful observation of species outside the United States, whether in their native ranges or in other new ranges—will remain a cornerstone of the prediction of the behavior of nonindigenous species before their entry into the United States. This practice is engrained in all current national and international systems for evaluation of the threats posed by nonindigenous species, such as the International Phytosanitary Protection Convention (FAO 1997, Pheloung et al. 1999).

Conclusion 2. There are currently no known broad scientific principles or reliable procedures for identifying the invasive potential of plants, plant pests, or biological control agents in new geographic ranges, but a concep-

tual basis exists for understanding invasions that could be developed into predictive principles.

The committee was not convinced that broadly successful methods for predicting invasiveness have been established. No reliable, all-inclusive, and tested list of potential invaders has been developed for plants, arthropods, or plant pathogens, nor has sufficient requisite information (species traits, circumstances of species' entrance, persistence, spread, rankings of new ranges by degree of vulnerability) been assembled to permit the identification of invaders. And there is not adequate information to quantify the uncertainties in the available predictive schemes.

Expert judgment—the synthetic ability of investigators who have long experience in monitoring the fate of species in new ranges—is now used to bridge the gap between a body of largely qualitative data and a determination of the probability of an organism's arrival and ability to establish. The collective experience of experts suggests that there is a conceptual basis for understanding invasions; the challenge is to transform judgment into transparent, repeatable, quantitative, and comprehensive predictive capability.

Conclusion 3. The inability to predict accurately which nonindigenous species will become invasive stems from a lack of comprehensive knowledge of the events that dictate species' immigration (arrival), persistence (survival), and invasion (proliferation and spread) in new environments. The requisite knowledge would be based on critical observation of the natural history of nonindigenous species and experiments designed specifically to evaluate nonindigenous species in the stochastic environments they encounter in new ranges.

It is not now possible for experts or predictive systems to be more unequivocal or definitive about invasiveness, because only part of the needed information is available. The committee found that specific, relevant information on the performance of species in new ranges is lacking, especially the results from experiments designed to evaluate the ability of nonindigenous species to persist and proliferate in a broad range of environmental conditions. Heretofore there has been insufficient attention to the fate of immigrant populations in demographic terms, except for scattered accounts of organisms released as agents of biological control and some plant pathogens.

Conclusion 4. Some data on the natural history of plant pests exist, but they often reside in grey literature and in datasets that are not easily accessible. Data on events that potentially lead to invasions are frequently collected by federal or state agencies in the course of pest surveys and inspections and after releases of biocontrol agents. Such collections need to be more comprehensive and need to be implemented on a quantitative, statistically sound

basis. Datasets need to be organized in a way that allows them to be analyzed and evaluated from the perspective of understanding invasiveness.

Much information has been gathered on the modes, pathways, and circumstances of organisms' dispersal on all geographic scales (Ridley 1930, van der Pijl 1969); indeed, these topics have been active arenas of scholarship among biologists for over a century. However, full value of this information is seldom obtained. Instead, we find basic references providing much the same litany of pathways, in the same detail, as was assembled decades earlier (Baker 1972, 1978, 1989).

The huge literature on the natural history of species is simultaneously a strength and a handicap in contributing to our understanding of the invasion process; much of the relevant information is mixed with ancillary information. A more systematized manner is needed to report and to access what is known about the natural history of potential immigrants, including species with a record of invasion, and results of localized pest surveys or evaluations of biocontrol releases. Such a system could provide a relatively rapid process for determining what is known about a species' natural history, native and current new ranges, habitat, hosts, prey, and impact. It could also minimize duplication of efforts, and identify priorities for research or survey activities.

RECOMMENDATIONS

In the following recommendations, the committee points to ways of strengthening the scientific basis for predicting the invasive potential of plant pests. The first three recommendations are directed toward USDA-APHIS and its regulatory activities because they are related to our understanding of the scientific basis of prediction. The other recommendations require action by USDA, other federal and state agencies, and the scientific community. Recommendations 4-7 are related to the documentation and standardization that are needed to understand invasions better. Recommendations 8-10 focus on needed research, and recommendations 11 and 12 point to the organizational infrastructure and scientific expertise that are needed to make headway in predicting invasions.

USDA-APHIS ACTIVITIES

Recommendation 1. The Port Information Network (PIN) database maintained by APHIS is a potentially valuable source of information for understanding the pathways by which potential invaders arrive at U.S. borders, but the utility and availability of the data could be substantially improved. Sampling methodology should be statistically designed and implemented consistently. Sampling protocols at ports and borders should be re-evaluated and revised as necessary to ensure that pest interception data are accurate

and meaningful. Data collection should be expanded to include vascular plants (in addition to those on the federal noxious weed and seed lists). Increased efforts are also needed to detect and identify pathogens consistently. Improved technology to detect hitchhiking insects and plant pathogens arriving with cargo, baggage, and related commodities could improve the utility of the PIN database (as well as reduce opportunities for new, potentially invasive pests to immigrate). The value of the database would be increased by including additional variables, such as a record of inspections that result in the detection of zero pests, some measure of the abundance of detected pests, and interceptions of nonquarantined pests. The data should be monitored consistently and regularly to identify and correct problems in data entry or maintenance. The PIN database should be accessible for analysis by investigators in universities and other agencies in collaboration with APHIS personnel who are familiar with the database.

There is great potential to learn more from the PIN data that vary in taxonomic status (such as individual species, families, guilds, orders, and class), spatial scale (such as selected ports, regions, or the entire United States) and temporal pattern. The complexity of the data and the background information needed to interpret it accurately require assistance from APHIS staff. APHIS should continue to collaborate in the analysis of the PIN data with scientists outside APHIS who have the relevant expertise and interests while working to make the database more independently accessible.

Recommendation 2. APHIS risk assessments combine a system of predicting an organism's arrival and establishment with an estimation of the possible consequences. The assessments are based on scientific concepts but contain uncertainties because of gaps in available information. To strengthen the overall prediction of invasive potential, the basis of APHIS risk assessments should be better documented, and assumptions made in each step should be listed and explained, so that independent experts can rationally compare conclusions about the likelihood of arrival, establishment, and impact. The assessment procedure should be transparent, repeatable, peer-reviewed, and updated to capture new information and enhance expert judgment.

Although risk assessments are used by APHIS to manage imports, they constitute the largest body of predictive systems so far attempted, insofar as they and related systems formed by other nations incorporate a set of assumptions about an organism's ability to arrive, establish, and cause damage. Those assumptions are tested after a decision to import (or not to import) a commodity or a new plant species. The arrival of a pest may or may not indicate a failure of the assessment, but examining the assumptions in light of new information or events requires that the assessments be explicitly stated.

Recommendation 3. The framework used by USDA to evaluate imported plants for potential release as forage, crops, soil reclamation, and ornamental landscaping should be expanded to include rapid multitiered evaluation of the hazards that these species might pose. Controlled experimental field screening for potentially invasive species should be pursued for species whose features are associated with establishment and rapid spread without cultivation and whose immigration history is unknown. Similar efforts to acquire life-history and population data in situations that approximate field settings would be beneficial in the case of nonindigenous insects and pathogens of concern, including species proposed for deliberate introduction.

A species' performance in environments it has not encountered before can be quantified only through experimentation (Hairston 1989, Mack 1996a). The paucity of our knowledge of the early stages of an invasion demonstrates the need for experimentation based on carefully constructed hypotheses about a species in specific ranges under measured environmental conditions.

A geographically broad network of experimental gardens should be established to identify species that could readily spread and persist. In addition to averting the release of a potentially invasive species, results of field trials would substantially enhance the ability to detect common patterns of plant performance in new environments. Extending those ideas to insects and pathogens, including those under consideration for deliberate introduction, would be valuable, although practical considerations associated with experiments in field settings may be more difficult to overcome.

DOCUMENTATION AND STANDARDIZATION

Recommendation 4. Information on invasions by plants and plant pests around the world should be assembled and updated regularly. Explicit information on new invasions in the United States—such as description of new locales, the partitioning of the species' genetic variation, and epidemiology of its spread—should be gathered and communicated more effectively to the scientific community; this information is essential in continually revising expert judgment. Careful recording of the circumstances of arrival, persistence, and invasion of nonindigenous species in the United States would substantially improve prediction and risk assessment.

First detection of the escape of a potentially harmful nonindigenous species in the United States and the rapid communication of this discovery among investigators, APHIS, land managers, and others interested in nonindigenous species are neither certain nor routine. Reporting of first detection is often restricted to informal alerts to subscribers on e-mail lists, and the reported information that is reported varies widely in completeness. If a high-profile invasive species, such as the Asian long-horned beetle or the zebra mussel, is detected, there may be an article in a major local newspaper. But finding a new nonindigenous plant rarely rates such a high-profile announcement. A more coherent system of reporting would centralize the responsibility for gathering and disseminating alerts about new species over an established network.

The need to make such information readily and instantly available via the World Wide Web has been identified repeatedly as a goal for invasion biology in general and international and national biosecurity in particular (Ewel et al. 1999, Ricciardi et al. 2000). Some databases are being assembled with those general goals in mind. The current U.S. Geological Survey database of invasive species in the United States, although modest in scope, is a productive step. Other government agencies and some professional organizations have begun compiling similar information (Ricciardi et al. 2000). Such purposeful data assembly and rapid communication will facilitate the continuing revision of our knowledge of the attributes, circumstances, and environments in which immigrant species arrive, are extirpated or persist, and occasionally become invasive. The information contributes directly toward construction of a predictive framework for invasions.

Recommendation 5. A literature synthesis on the natural history of potential immigrant species, similar to the "Biology of Weeds" series published by the *Canadian Journal of Plant Science*, should be established, standardized, and made accessible via the Internet.

The natural history of plants proposed for introduction into the United States should be much better documented. The long-running "Biology of Weeds" series of publications in the *Canadian Journal of Plant Science* and the "Biological Flora of the British Isles" series in the *Journal of Ecology* each deal with one species (or at most a few closely related congeners) and illustrate an approach that the committee recommends. All the natural history and ecology known for the species is organized in these publications under standardized headings, such as "phenology", "habitat", "geographic ranges" (with maps), and "predators and parasites". The articles reflect exhaustive searches of the literature to assemble a comprehensive record of knowledge for species (see Ricciardi et al. 2000).

Such literature syntheses for potential immigrant species should be broadened. We cannot and do not need to know the detailed life history of every species on the planet. But deliberately augmenting existing systems, as illustrated by those two journal series, would substantially improve expert judgment. In that regard, cooperation with biologists outside the United States, especially in nations that have species likely to arrive in the United States (China is a prime example), in the assembly of the relevant information about their biota should be encouraged and supported.

Recommendation 6. Information on the structure and composition of natural ecosystems in North America (and the disturbance regimes within

them) should be reinterpreted by the scientific community to analyze these ecosystems' vulnerability to biotic invasion. Attention should be paid to identifying groups of native species that could be vulnerable or could facilitate the establishment of nonindigenous species.

Ecologists have actively described and quantified the natural communities of the United States for a century (Curtis 1959, Barbour and Major 1988, Franklin and Dyrness 1988). Although varying considerably in taxonomic and ecological thoroughness, this body of information is nonetheless impressive for its geographic and environmental comprehensiveness. Furthermore, attempts to categorize the different vulnerabilities of communities to biotic invasion have begun (Lonsdale 1999). To answer the hypothetical question of which species will invade which communities, we need to view the communities from the standpoint of the fundamental processes, forces, and factors that dictate community composition (Tilman 1997, Naeem et al. 2000). What influences the species composition, including nonplant and microbial species of each community, and provides any restriction or vulnerability to future species additions? Answers to such questions require not so much new community analyses as reinterpretation of existing information.

To predict future invaders, we need a better understanding of the functional groups—taxonomically unrelated species that perform similar community roles—in communities (for example, Metzger 2000). We need to identify communities whose lack of particular functional groups makes them vulnerable to the entry and establishment of nonindigenous species that perform those roles. For example, a community with little representation by plants with nitrogen-fixing nodules may be vulnerable to the arrival and persistence of nonindigenous species that are nitrogen fixers (Vitousek et al. 1987, Vitousek and Walker 1989).

Recommendation 7. A consensus on procedures to measure the impact of invasive species should be forged in the scientific and regulatory communities, and there should be more reporting of impacts of invasive species with standardized measures.

Without consistent measures of impact, conclusions about the potential consequences of an invasive plant pest will remain vague; this will hamper the incorporation of impact into predictive systems, including risk assessments. Establishing a common language for measures that characterize impact at different levels of biological organization, from effects on individuals to ecosystems, is essential. Measures of economic and social impact are also needed.

RESEARCH

Recommendation 8. Research on host specificity among pathogens and the correlation of some life-history traits (such as dispersal mode, reproductive

system, and host range) with their documented ability to invade should be undertaken in relation to potential environments in new regions or areas. Question-oriented experimentation to elucidate relationships among species' traits and their new environments and hosts should be supported.

Long-term investigation in plant pathology has provided voluminous information on the intimate host-pathogen associations that form reliable guides for future attack on the same hosts, even if pathogen and host meet in new geographic ranges (Parry 1990, Lucas 1998). Similar intimate associations occur among many nonindigenous phytophagous insects and their host plants. These interactions form the basis for strong predictions of whether an immigrant pathogen or arthropod will present a threat. Collection of this information needs to be supported. In contrast, few plants display such detrimental interaction with a restricted group of other plant species. And the link between plant species' traits and their invasiveness has often proved difficult to identify. Nevertheless, life-history traits ultimately do influence the ability of a nonindigenous species to persist in a new range, and this link should be explored more fully, especially for insects and pathogens (Rejmanek and Richardson 1996, Reichard and Hamilton 1997).

In addition, of species that have the potential to immigrate and become invasive, little is known about many *until* they inflict harm. For instance, we know much about the biology of *Melaleuca quinquenervia* (melaleuca), *Lantana camara* (lantana), *Salvina molesta* (karibaweed), and *Euphorbia esula* (leafy spurge), but little or nothing about their apparently noninvasive congeners. This gap in our information denies us a powerful comparative tool with which we could potentially glean much insight into the performance of invasive species by understanding how specifically and quantitatively they differ from their closest relatives. Barrett (1979, 1980) explained much of the invasive ability of *Eichornia crassipes* (water hyacinth) by comparing the mating system and vegetative propagation of this horrific pest in comparison with its seemingly harmless congeners. Investigating the ecology of the congeners of invasive species could become a powerful tool for identifying characters or attributes of invaders that directly contribute to their invasive ability (Barrett 1979,1980, Schierenbeck et al. 1995).

Studies of associations and interactions between invasive species, particularly vectors and pathogens, can also benefit from an understanding of congeners. For example, beech bark disease is a lethal disease complex in which a scale insect, *Cryptococcus fagisuga,* predisposes beech bark to infection by several taxa of the fungal genus *Nectria*. Although a native *Nectria* species complexes with *C. fagisuga* to cause beech bark disease, an introduced species of *Nectria (N. coccinea* var. *coccinea ectria)* now predominates in most areas of the Northeast. In areas newly invaded by the scale insect, it appears to replace the native *Nectria* species rapidly, raising questions about the association of vectors with closely related pathogens and about the significance of the disease's impact if only the insect and not the fungus had been introduced (Mahoney et al. 1999).

Recommendation 9. The release of nonindigenous organisms for biological control presents an opportunity to collect detailed demographic data on immigrant populations from the moment of their introduction. A substantial effort should be made to document the fate of these organisms, including the efficacy of the introduced organism on the target pest and on nontarget species, as a guide to the performance of unintended releases and as a mechanism to improve risk assessment in deliberate introductions of nonindigenous species.

Understanding and quantifying the forces that cause populations to become extinct, especially by natural forces in a new range, will prove central to building our understanding of the invasion process (Harper 1982, Mack et al. 2000). The comparatively little that is known in quantitative terms about invasions has been learned by following the rare event of a nonindigenous species that actually develops an invasion. We also need comprehensive knowledge of the circumstances under which almost all immigrants go extinct—whether in transit, at the point of entry, or as adventive species in a new range (Mack 2000)—or those that decline numerically after having seemingly attained persistence (Simpson 1984). Releases of organisms for biological control are, in effect, experiments that assess the performance of species in their native range and simultaneously in potential new ranges. Following the fate of these populations could be invaluable in that the genetic composition, precise native range, size of the founder population, and time of release are all probably known (Grevstad 1999a,b).

Recommendation 10. Plants native to the United States that are growing in other countries, such as in botanical gardens and arboretums, should be monitored to determine the species to which they are susceptible and to evaluate the potential for these species to arrive in the United States. The severity of the damage to native U.S. plants by pathogens, arthropods, and other taxa, and the abiotic and biotic forces that contribute actively to the damage, should be documented.

Expert judgment could be improved substantially through a deliberate and expanded effort to assess species that attack U.S. crops and native plants in ranges outside the United States. Cereal crops, cotton, soybeans, some pines, and numerous ornamental trees, shrubs, and herbaceous plants are grown worldwide and are exposed to pests not currently found in the United States. Reports of the organisms that attack these plants are invaluable when coupled with some estimate of the potential for the harmful species to arrive in the United States (Hewitt and Chiarappa 1977). For instance, the potential hazard of introduction of the Russian wheat aphid and plum pox was understood, on the basis of foreign experience, before these species arrived in the United States. But too many species of plant pathogens and phytophagous arthropods occur outside the United States to evaluate the potential damage from all of them. The list of species that deserve careful attention would be substantially reduced and focused by monitoring of pests of U.S. crops and native U.S. species growing in foreign ranges. Such monitoring would provide early warning of nonindigenous species that, if introduced, would become threats in the United States. Australia has already begun a similar form of assessment for its invaluable native eucalypts growing in Southeast Asia, and its experience could form a valuable precedent (Wylie and Floyd 1999).

INFRASTRUCTURE AND EXPERTISE

Recommendation 11. A central repository of information relevant to immigrant species would accelerate efforts to strengthen the scientific basis of predicting invasion. Information collected by federal, state, and international agencies, academic researchers, and others should be brought together in a single information facility or service so that it can be evaluated collectively, to permit the construction of needed datasets and the design of appropriate experiments, and to document the circumstances surrounding invasions.

The considerable information that is required to build comprehensive predictions of invasion would be best assembled by a central authority with strong ties to and guidance from user groups. The information needed is so diverse that only a facility with a specific mission to gather it and make it available will be effective in achieving an understanding of invasion and an ability to predict it. Requests for a centralized authority on biological invasion have been made by many in the scientific community (Ewel et al. 1999, Schmitz and Simberloff 2001). Information that could be collected by such a facility includes much of the types suggested in this report, such as the documentation of newly detected nonindigenous organisms in the United States, information on biotic invasions around the world, and the results of organisms released for biological control. The creation of a central facility of this type would help with efforts to predict invasive species and is consistent with the goals of the National Invasive Species Council (2001).

Recommendation 12. Focused scientific investigation is inadequate on nonindigenous species and prospective new environments from the overarching perspective of invasive potential. Multidisciplinary collaboration should be encouraged and supported among scientists with taxonomic expertise and those who specialize in population biology, community ecology, epidemiology, and simulation modeling. Multidisciplinary training of established and new investigators is needed to provide the expertise needed to make the study of invasion biology predictive.

In spite of a long history of interest in biological invasion, scientific inquiry in invasion is still nascent. Progress in understanding and predicting invasion will depend on how well the insights of investigators with diverse training can be coalesced and directed to decipher the myriad combinations of immigrant species, new environments, and novel circumstances that can produce biological invasion. The last 10 years has seen the emergence of a broad consensus that the prediction of biological invasion is of pressing national need (U.S. Congress 1993, Clinton 1999). It will take some time, however, to generate the predictive principles on which policy-makers, regulators, the scientific community and the public can have confidence.

On the basis on the current state of prediction of the fate and effect of nonindigenous species, the committee concludes that action needs to be initiated now to replace the largely retrospective or anecdote-based prediction process with a system derived from experimentation. (In a larger sense, science has always progressed in this manner—first a long period of natural history and observation, and then continuing, deliberate, question-based experimentation.) This sense of urgency in moving in a deliberate manner from expert judgment to prediction on the basis of experimentation is driven by the pressing societal need to deal fairly, adequately, and swiftly with an unparalleled volume and scope of trade involving nonindigenous species. These are policy issues, based in science, that cannot be left lingering and cannot be resolved through happenstance investigation.

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Glossary

abiotic: physical properties of an environment, such as climate, soils, atmospheric gases.

adventive: nonindigenous species which has recently arrived or which appears to be a temporary resident in a new range; its persistence has not been determined.

allele dynamics: the interactions of alleles with each other.

alleles: any number of variants of a single gene.

allelopathy: the production and emittance of organic compounds by an organism that causes detrimental consequences for its neighbors.

allopatric: two or more species having nonoverlapping ranges of distribution.

annual: an organism that completes its life cycle in a year or less.

antipodal: opposites; refers to any objects (such as chromosomes) that are at diametrically opposite extremes.

apomixis: the development of a seed without fertilization.

arrhenotokous: capable of producing male offspring only, as in worker bees and some sawflies.

asexual reproduction: any reproduction not involving the fusion of gametes.

autotroph: an organism capable of self-nourishment, such as a plant nourishing itself by photosynthesis.

avirulence gene: a gene that infers the inability to infect another organism.

basic reproduction number ($\mathbf{R_o}$): the average number of offspring or infectious units from a single organism or infectious agent.

biological control: control of an invasive species by the introduction of a predator, grazer, or pathogen of that species.

biotic: any process or phenomenon that is caused by living organisms.

carrying capacity: the theoretical maximum number of individuals in a population that can be supported by a defined set of conditions in an environment.

cline: a geographic gradient in the frequency of a gene.

confamilial: belonging to the same family.

congeners: members of the same genus.

congeneric: referring to members of the same genus.

conspecific: referring to members of the same species.

cryptogam: plants and plant-like organisms that do not reproduce with seeds and do not produce flowers, such as ferns, mosses, fungi, and algae.

demographic: refers to any attribute or process relating to a population.

deterministic growth rate (λ): a growth rate that has only one outcome as defined by the parameters or conditions under which the population occurs.

diapause: a state of arrested growth or development, usually applied only to insects.

dichogamy: flowers that are functionally male first, then develop female structures.

dioecious: producing male and female structures on two separate plants within the same species.

dioecy: in plants, the possession of male and female structures on separate individuals.

diploid: possession of two full sets of genes and two sets of chromosomes; one set from the mother, one from the father.

dsRNA: double stranded ribonucleic acid.

ectophagous: feeding on the outside of the host.

endophagous: feeding on the internal organs or at least within the body of the host.

endophytic: fungi that reside within plant cells, or plants that live within other plants.

entomophagous: insect-feeding.

epiphyte: a plant that grows on another plant nonparasitically, or grows on an object.

establishment: permanent self-maintenance of a population without additional members arriving through immigration.

exploitation competition: competition in which resources obtained by one organism, population, or species results in a lowered resource availability to another organism, population, or species.

floras/faunas: the collective assembly of all plants (floras) or animals (faunas) within a prescribed area and within a prescribed taxonomic group (for example all insect species in the United States).

founder: an organism which gives rise to a new populations.

genetic drift: changes in allelic frequency due to sampling error; that is, changes in frequency that result because the genes appearing in offspring are not a perfectly representative sampling of the parental genes (such as occurs in small populations).

genotypes: the genetic constitution of an individual or group.

haustellate: having a tubular organ adapted for sucking blood or the juices of plants.

herbivorous: refers to those animals that feed or graze on living plant material, usually in reference to non-reproductive tissue (i.e., leaves, stems).

heterogamy: alteration of sexual reproduction with parthenogenesis.

hermaphrodite: an organism that possesses the reproductive organs of both sexes.

heterozygosity: the proportion of the individuals in a population that are heterozygotes; that is, those individuals that have two different alleles at a locus.

homozygous: having two copies of the same allele at a genetic locus.

indigenous: native to a prescribed geographic range.

interference competition: competition between any two individuals in which one physically excludes or prohibits another from gaining a resource in short supply.

intrinsic rate of increase (r): maximum growth rate of a population, estimated as a birth rate minus the death rate; the net increase in the population.

inverse density dependence: increase in fitness with increases in density (birth rates rise, mortality rates drop).

invasion (biotic or biological): a phenomenon in which a nonindigenous species arrives in a new range in which it establishes, proliferates, spreads, and causes broadly-defined detrimental consequences in the environment.

lag phase: phase in the typical cycle of population growth, when there is little or no growth, between introduction of an organism and exponential (log) growth.

larval: in connection with arthropods, the immature instars, that is, stages in development.

logistic curve: growth curve characterized by oscillation of population growth at a level below the carry capacity.

log phase: phase in the typical cycle of population growth, between lag phase and decline, when a population grows exponentially.

mandibulate: chewing, in reference to insects that chew prey with those mouth-parts called mandibles.

mean population growth rate: the average rate by which a population changes size.

mesic: having or characterized by a moderate amount of moisture.

mesophytic: referring to intermediate environmental conditions.

monoecious: bearing the reproductive structures of both parents on the same plant.

monophagous: feeding on a single prey or forage species.

Moran effect: a spatially correlated density independent perturbation, such as weather, which occurs across populations.

multilocus genotype: a genotype that results in a trait or traits from the expression of genes at multiple locations within the genome of an organism.

mutational variance: variance in the genetic make-up of a population due to mutations in individuals' chromosomal DNA.

naturalization: the establishment of a nonindigenous population in a new range; used mainly in connection with plants.

net reproductive rate: average number of offspring an individual in a population will produce in his/her lifetime.

nonindigenous: not native; refers to a species, population, organism that occurs at a locale that is not part of its native range.

oligophagous: feeds on a few or several prey or forage species.

oviposition: passage of the arthropod egg from the oviducts to outside the arthropod; egg-laying.

pathotype: an infrasubspecific classification of a pathogen distinguished from others of the species by its pathogenicity on a specific host(s).

parasitoids: insects that initially behave as a parasite but eventually act as a predator and devour their host.

parthenogenetic: production of individuals from unfertilized eggs.

perennials: organisms that may (and usually must) survive several years in order to reproduce.

phenological synchrony: correspondence between traits in becoming active at the same season.

phenotype: the observable characteristics of an organism.

phenotypic plasticity: the phenomenon of organisms displaying a range of phenotypes from the same genotype.

phytophagous: feeding on plants.

phytosanitary: related to ensuring plant health.

plasticity: the capacity of organisms with the same genotype to vary in developmental pattern, in phenotype, or in behavior according to varying environmental conditions.

polyphagous: feeds on many prey or forage species.

polyploidy: possessing more than two sets of genes and chromosomes.

population: a group of genetically related members of the same species living within a prescribed space or range within a prescribed time frame.

propagules: seeds, eggs, spores or other resting stages that are capable of being transported.

physiognomic: literally the morphology of a plant community; refers to the number and characteristic shape of the layers of plants if the community were viewed in cross-section.

predatory guild: a group of several types of predators that feed on a particular developmental stage of a pest.

race: a genetically or geographically distinct subgroup of a species.

ruderal: highly disturbed areas, such as rubbish heaps.

selfer: an organism that does not require a sexual partner to contribute either egg or sperm; the organism contains both sexes.

stochastic: random, involving chance or probability.

sympatric: referring to speciation within the same geographical area.

true annual population: a population that replicates one time per year.

univoltine: one generation per year, used in connection with arthropods.

voltinism: the frequency or number of annual broods.

About the Authors

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