INVASIVE SPECIES

Vectors and Management Strategies

EDITED BY

GREGORY M. RUIZ AND JAMES T. CARLTON

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Cover caption: Between 1890 and 1914 Britain built two-thirds of the world's ships and transported 50 percent of the world's seaborne trade. The cover figure shows principal steamer routes and coaling stations as plotted on an Admiralty map of 1889, suggesting the scale and complexity of the global movement of ships—and of the organisms they transported. Modified from A. N. Porter, ed., 1991, *Atlas of British Overseas Expansion.* (Simon & Schuster).

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Preface

Interest in the science and management of biological invasions has expanded rapidly in the past decade. Most invasions result from transport of organisms by human activities from one place to another, whether intentional or unintentional, allowing species to become established in new geographic regions. A steep rise in the number and impact of invasions has been observed for virtually all major habitats on Earth (Baskin 2002), propelling public concern, scientific interest, and calls for policy and management actions. Effective policy and management strategies—aimed at reducing the considerable ecological, economic, and human-health risks of invasions—depend upon a solid understanding of transfer mechanisms (vectors). In short, a scientific understanding of why, how, when, and where species are transported provides a critical foundation for vector management.

This volume explores the current knowledge base and policies surrounding invasion vectors, presenting updated contributions from a conference held November 8-11, 1999, at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland. The "Conference on Pathways of Nonindigenous Species" was part of a series of workshops of the first phase of the Global Invasive Species Programme (GISP). GISP Phase I was developed in 1997 as a collaborative, international effort to address concerns about alien species invasions by initiating a scientifically based global strategy to understand invasions and limit their unwanted impacts. Phase I (Mooney 1999; http://globalecology.stanford.edu/DGE/Gisp) consisted of 11 program components and involved a diverse group of international science and policy experts. The goals of Phase I included (a) assembling information on patterns, prevention, and management of invasions across geographic regions, ecosystems, and taxonomic groups, and (b) distributing this information through a variety of avenues to governments, communities, and scientists.

A key component of GISP focuses on understanding invasion vectors and identifying management strategies to prevent invasions. To advance this component, we organized a conference to assess invasion vectors and vector management in terrestrial, freshwater, and marine ecosystems for major taxonomic groups in a variety of regions around the world. Information presented at this conference was further developed and expanded to create this volume.

Structure of the Book

This book is divided into three sections, each with a different purpose. The first section, comprised of nine chapters, highlights our present understanding about the operation of vectors and forms the book's data foundation. Examined are invasion causes, routes, and vectors across a diverse range of habitats and taxonomic groups. The major vectors that have led to the homogenization of terrestrial plants (especially "weeds"), fungi, insects, and vertebrates are examined in the first four chapters. Bridging both land and freshwater is an examination of the invasion histories of terrestrial and aquatic gastropod mollusks (snails and slugs), while a separate chapter focuses on freshwater fish, amphibians, reptiles, and mammal invasions. Two chapters concern the marine environment, considering invertebrate and plant invasions. The last chapter in this section focuses on an analysis of shipping vectors that serve to transport species into the world's largest freshwater ecosystems, the Laurentian Great Lakes of North America.

This first section does not attempt a comprehensive analysis that includes all guilds or taxonomic groups (e.g., freshwater macrophytes, phytoplankton, and various freshwater and terrestrial invertebrates are not covered here), but the data provided among chapters offer a detailed look at how literally thousands of species were transferred—and often are still being moved—around the world. The groups not treated here are important; fortunately, review essays are now available for many of them.

The second section consists of eight chapters that examine different approaches to management and policy, geared at reducing the likelihood of invasions and invasion impacts associated with vectors. In the first five chapters, contributors examine how vectors have been, are, or could be intercepted and managed. These chapters are focused upon specific countries as case histories, including Australia, New Zealand, South Africa, and the United States. An important bridging chapter that links the book's first and second sections is a view from South Africa, where vectors (such as forestry, horticulture, and shipping, and intentional releases of birds, mammals, and fishes) form the basis for modern perspectives of legislation and management action. Each chapter in this section takes a somewhat different approach—based upon the taxonomic array of species being tackled and upon national experience—but form a fascinating overview of both divergent and complementary strategies. The final three chapters address the emerging field of risk analysis, and its two major components, risk assessment and risk management. These three chapters each take a different focus, using a species-based approach, a pathways-based approach, and a "generic" approach that takes into account both species and pathways.

The final section consists of a single chapter as an overview and synthesis of vector ecology, drawing on the previous chapters and additional material. The goal of this last section is to integrate much of the information across previous chapters to develop a broad-based, conceptual framework and next steps for vector management.

Terminology

While invasion terminology was discussed at the conference, we did not attempt to standardize authors' usages across chapters of specific terms for the transport of organisms through human action. Elsewhere (Carlton and Ruiz 2004) we have suggested a potential framework to standardize terms and definitions associated with vector science. This framework focuses on the terms used for causes (why a species is transported, whether accidental or deliberate), purposes (why a species is deliberately introduced), routes (the geographic path over which a species is transported), corridors (the physical conduit over or through which the vector moves within the route, such as footpaths, roads, and railroad beds), and vectors (how a species is transported—that is, the physical means or agents). Not all of our authors use these terms in the same way, but within the context of any one chapter, definitions and applications of words and concepts are clearly provided.

In similar fashion, the terminology used to characterize non-native species is extensive. Common terms include aliens, exotics, invaders, nonindigenous species, introduced species, immigrants, translocated species, naturalized species, colonists, adventives, neophytes, weeds, imports, and invasive species. The usage and particular meaning vary among taxonomic groups, geographic regions, as well as among individual scientists, managers, and policy-makers. This variation is perhaps most evident in the usage of the term "invasive," which often refers to species that spread or cause significant impacts (for discussion see reviews by Pyšek, 1995, Eser 1998, Richardson et al. 2000, Carlton 2002). For example, invasive plant species are considered by many to be those that establish self-sustaining populations and then undergo spread. For other taxonomic groups, and in the political arena, invasive species are frequently considered to be those organisms that cause significant and unwanted ecological, economic, or human-health impacts, having a distinctly negative connotation. As with transport activities, we have not attempted to standardize terminology used among chapters to describe non-native species.

We have used the term "invasive species" in the book title, in large part to be consistent with this focus and usage of the Global Invasive Species Programme. This term has the advantage of widespread recognition, both by the public and scientists, as being associated generally with colonization by non-native species. However, precise definitions of "invasive" remain in flux (as above; see Carlton 2002), as attributes of established populations—in terms of spread and impact—fall along a continuum (instead of binary bins). Moreover, the potential or realized attributes of many, if not most, non-native species are simply not known—within their native or newly colonized territories—further confounding such classification.

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We are most grateful to Harold Mooney for his encouragement and guidance throughout Phase I. We thank the many colleagues who reviewed chapters, and particularly Richard Mack, who both performed yeoman work as a reviewer of many chapters, and provided motivation and inspiration in assembling this book. We are in addition thankful to members of the Marine Invasion Research Laboratory at SERC, and especially Kelly Lion, who were instrumental in assisting us with all aspects of organizing the Conference. We also benefited greatly from editorial assistance by Monaca Noble and Kelly Lyles in producing the present volume. Barbara Dean, Barbara Youngblood and Meg Weaver, Island Press, patiently escorted us through the labyrinth of the editorial process and final book production.

Finally, we wish to thank the conference participants and sponsors for the opportunity to explore the many, complex facets of vector ecology and management. The conference was sponsored and funded by the Global Environment Facility, Scientific Committee on Problems of the Environment (SCOPE), Smithsonian Institution, and the United States Geological Survey (USGS).

—Gregory M. Ruiz and James T. Carlton

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Contents

Part I

INVASION CAUSES, ROUTES, AND VECTORS:

Spatial and Temporal Patterns in Terrestrial, Freshwater, and Marine Ecosystems

Chapter 1

Global Plant Dispersal, Naturalization, and Invasion: Pathways, Modes, and Circumstances

Richard N. Mack

"He who defends everything, defends nothing." This quote from the philosopher-king and military strategist Frederick the Great may seem an oblique manner by which to begin a chapter on the global dispersal of plants. Its relevance here lies in the goal of predicting global plant dispersal as a means to curb, if not prevent altogether, the entry of species in new ranges in which they could be invasive (*sensu* Mack et al. 2000). Both military defense and the quarantine for nonindigenous species deal with the pathways, modes (or conveyances), and circumstances of the foreigners' arrival as well as their number and composition. More specific, the questions for the military commander and for his/her plant quarantine counterpart follow a similar track. By what route(s) or pathway(s) will the foreigners arrive? Where within the defended territory will they enter? How many will initially and subsequently arrive? How will they arrive, that is, by what mode? What circumstances and features of the new locale will foster or hamper their persistence, geographic spread, and the consequences of their actions? Equally important but largely outside the scope of topics considered here is the character of the aliens; that is, will they be alike and respond similarly to all factors in the defended territory?

Whether dealing with human intruders or potentially harmful plant immigrants, answering all these questions correctly is daunting, especially when the potential entry points are numerous and the threat of entry is long term. The global dispersal of plants is a huge topic with many components. I do not attempt here to cover this subject in the comprehensive manner that Ridley achieved in his 1930 classic work or the more focused accounts by Guppy (1906) and van der Pijl (1969). Instead, I outline (1) pathways of both historic and modern importance to plant dispersal that have led to naturalization and invasion. (2) Drawing on the myriad modes by which plants are moved long distances, I illustrate several modes that have long attracted biologists (e.g., solid ballast, commercial seed lots) and then (3) outline the historic and modern consequences of the chief mode by which nonindigenous plants enter new ranges—deliberate introductions.

PATHWAYS OF PLANT DISPERSAL

I use the term pathway or route in a strict sense here: advance or progression in a particular direction, regardless of the mode (i.e., conveyance) that disperses plants along that pathway. By definition then, a pathway has a starting point and one or a series of destinations, as opposed to a probability distribution of destinations.

Natural Pathways

Atmospheric, oceanic, and river currents have always formed pathways or routes for plant dispersal. For instance, the Gulf Stream has carried seeds and plant propagules not only through the Caribbean but also as far as the British Isles. One consequence of this long-term dispersal has been the arrival of many subtropical species in the Scilly Isles, southwest of the main islands of Britain (Lousley 1971). Similar long-distance dispersal has facilitated the spread of mangrove species through Oceania and elsewhere (Murray 1986). Such movement can be highly directional: off the western coast of North America, the California Current carries plant flotsam in a distinctly southerly direction each summer. Alternatively, species are not as likely to reach a new range along these natural pathways, if the range lies outside the path of prevailing currents.

Ocean and air currents, of course, continue to affect plant distribution; their influence on the dynamic composition of any flora is a direct function of the frequency with which they carry plants to new ranges (Ridley 1930). Not surprisingly, strand and shoreline species commonly immigrate in this manner (Smith 1999). The sprawling morning glory, *Ipomoea pes-caprae,* is a cosmopolitan subtropical/tropical shoreline species (Ridley 1930); its huge geographic distribution is a direct consequence of its floating seed and tolerance for sandy, salt-spray environments. Even among species not confined to shorelines, natural forces continue to transport species across impressive distances. Natural forces have apparently dispersed plants from Australia to New Zealand in modern times (Mack and Lonsdale 2001); these immigrations have produced adventives and possibly some naturalizations but no invasions. The role that the natural forces of moving air and water play today in changing plant distributions is small, compared with the role of humans. These natural forces are not feeble, just infrequent, in their global impact.

Pathways Developed by Humans

The human dispersal of plants has long followed many natural pathways, especially when human transport was substantially dependent on wind and water currents. The Gulf Stream along with the weaker Canary Current off North Africa and the westerly South Equatorial Current formed a great triangular route for sailing ships between Europe, West Africa, and the Caribbean that was in full swing by the early eighteenth century (Viola and Margolis 1991). Thus, ships augmented flotsam and other living rafts as conveyors of plants from Africa to South America and the Caribbean. The list of locations to which plants could be carried by ships was greatly expanded with the well-known advances in ship construction and navigation, beginning in the late fifteenth century and the later advent of steam-powered ships. It is hard to overestimate the increased likelihood of transoceanic plant dispersal as a result of these innovations. In effect, any two anchorages now potentially share a connecting pathway. As a result, species have been introduced to new ranges that they would not have reached by ocean currents alone; for example, species native to temperate Britain reached temperate New Zealand and vice versa (Good 1964).

With the enormous versatility of steamship travel, webs of transoceanic pathways soon became well established. These routes were shaped by the desire to speed commerce between trading partners, which were often European (and later American) nations and their overseas colonies. Even before the advent of steamships, a path for plant dispersal had developed between western Europe and the North American eastern seaboard and soon thereafter between the Netherlands and Britain and their colonies at the Cape of Good Hope, in the South China Sea, and Australia (Mack 1999 and references therein). These routes initially relied on ocean and wind currents; they multiplied as coaling stations were established. For instance, by 1889 Britain alone had established with its colonies and other trading partners 156 coaling stations that spanned the world (Porter

1991) (Fig. 1.1). France, Germany, Portugal, and Spain also maintained ports and connecting routes with their overseas colonies (Emmer and Gaastra 1996).

With steamships, landfalls that were exceptionally remote and unlikely to receive plant immigrants by natural forces (e.g., Ascension and St. Helena Islands in the southern Atlantic) became the recipients of many deliberately and accidentally introduced plants (Cronk 1989). Furthermore, along these webs of routes thousands of plant species were efficiently moved within colonial empires. By the late nineteenth century Britain had established botanical gardens at key locations worldwide (e.g., Calcutta, Cape Town, Hobart, Port of Spain, Singapore) (McCracken 1997). These facilities became bases for plant collection from which newly discovered species could be shuttled within the British Empire via London's Kew Gardens—an early hub-and-spoke transportation network. Never before had plant immigration operated on such a massive scale, replete with test gardens in potential new ranges (McCracken 1997). As discussed below, scores of species that were transported along pathways developed in the nineteenth century among Europe, North America, and Europe's colonies later became naturalized; some have become invasive (e.g., the woody plants, *Rhododendron ponticum, Acacia ieucocephala, Leucaena nilotica,* and *Lantana camara*). The tradition of massive worldwide plant exchanges can be traced to the development of these colonial programs, beginning as early as 1600 (Kloot 1987, Mack 1991, 1999, McCracken 1997).

The spread of plants was extended inland with the growth of canals (Mills et al. 2000) and, later, railroads (Dewey 1896, Mack 1991). Canals were seen as essential routes for eighteenth-century commerce in the United States, a view that continued until they were largely supplanted by railroads at the end of the nineteenth century. In the meantime, navigable canal networks laced the interior of the eastern United States and provided a mode for both deliberate and inadvertent spread of nonindigenous plants. Reconstructing the nineteenth-century spread for accidental introductions along canals is necessarily circumstantial and relies on the collection history of these species alongside or near old canal routes. Invasion by the aquatic herb *Lythrum salicaria* (purple loosestrife) has been documented in this manner. Thompson et al. (1987) contend that with the exception of the canal system in interior Pennsylvania, the early-nineteenth-century inland spread of *L. salicaria* in the northeastern United States was tied closely to canal traffic moving from navigable East Coast estuaries. And most sites of purple loosestrife's pre-1880 establishment in the region were along the Erie Canal, which bisected New York and the Delaware & Raritan Canal, which bisected New Jersey (Thompson et al.

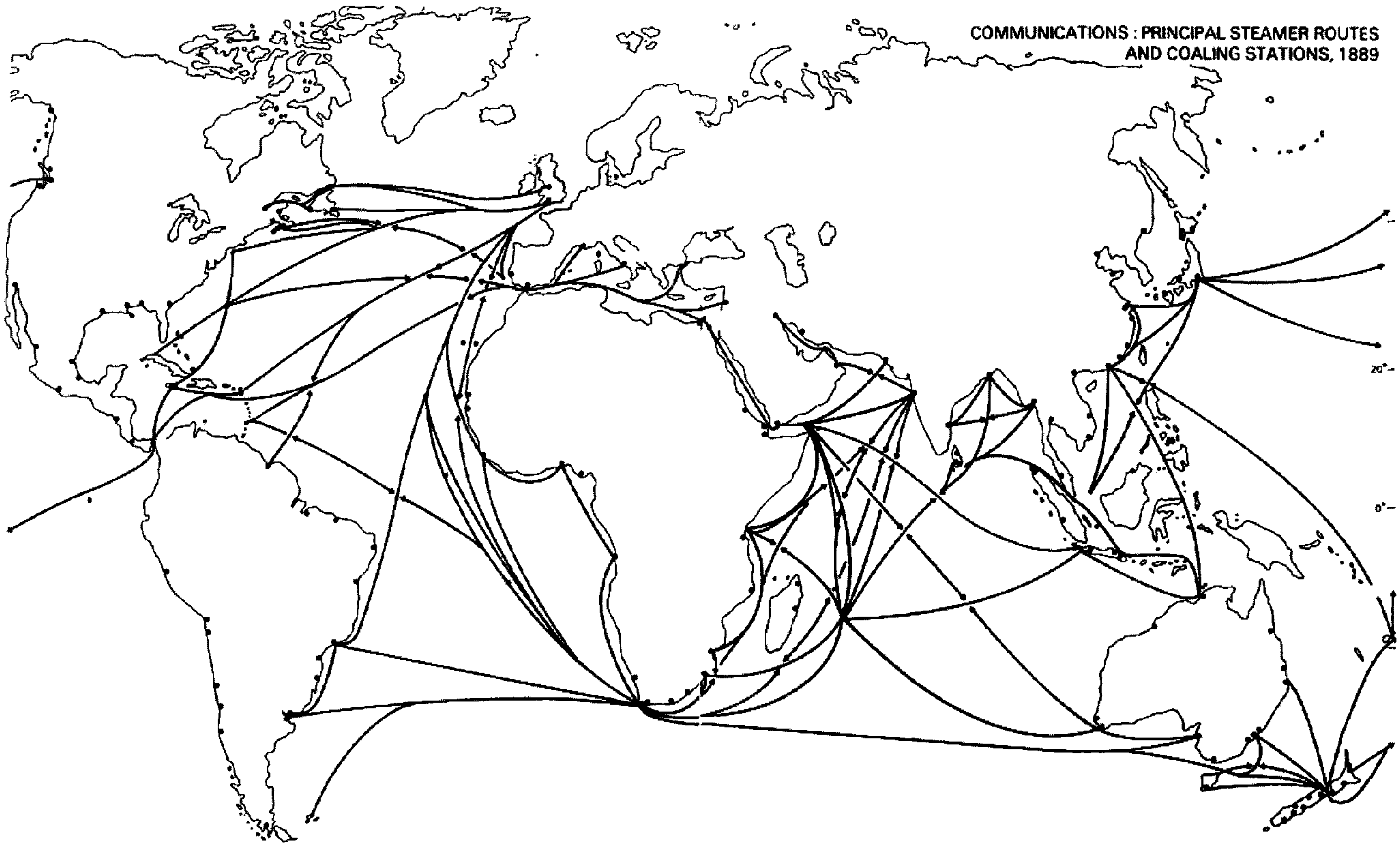

FIGURE 1.1. Principal steamer routes and coaling stations (holding at least 500 tons) within the British maritime system in 1889 (Porter 1991). Britain's colonies and trading partners spanned the globe and made the rapid transport of plants a routine procedure.