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Global Plant Invasions

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 Springer

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Foreword

I have spent a good portion of my life studying invasive plant biology and ecology with the goal of developing effective management strategies and programs. Though most of my work has been in North America, I have had the good fortune to travel the world to see the ecological responses and impacts of invasive plants under a variety of climatic and environmental conditions. In one of my international trips to southern China with Dr. David Clements (primary editor of this book) and Dr. Leslie Weston (chapter author), we observed the devastating effects of the invasive mile-a-minute weed (*Mikania micrantha*) on a wide variety of crops and the extensive invasion of southern China forests by Crofton weed *Ageratina adenophora* (or *Eupatorium adenophorum*). My visit to China and other areas of the world demonstrated to me the importance of a global understanding of the ecology and impacts of invasive plants to better prevent, understand, manage, and develop appropriate policies to reduce their environmental and economic effects.

This book provides the most comprehensive global perspective on invasive plants ever published. Its coordination by the editors is a monumental effort, considering the number of authors and their wide range of languages and regions in the world. The task, however, was well worth the effort as the book gives a perspective of invasive plants from nearly every continent on the globe, apart from Antarctica. The authors represent many of the leading invasive plant experts and authorities from 23 countries of North, South, and Central America, Europe, Asia, Africa, and Australia. The book is primarily organized by large land areas or continents but has special chapters on the uniqueness of island and mountain plant invasions, as well as invasion processes, history of global spread, climate change, impacts, advances in management, global strategies, and thoughts on the future. The chapters on global regions provide exceptional coverage of pathways of introduction; distributions with respect to countries or climatic zones; plant traits and life histories that increase invasion success; impacts, both economic and environmental; and policies and legislation important to each region. Having a fascination with history, I found the historical perspective of invasive plant introductions in a variety of continents and countries particularly interesting. These should provide valuable insights on future introductions and spread.

The authors give an outstanding global perspective of invasive plants from each region, which is critical to understanding invasive plants even at a local level. For example, *Ulex europaeus* is native to cooler maritime regions in the western coastal areas of continental Europe and the British Isles. It has

become invasive in many regions of the world in a similar habitat, including the California coast, South and Central America, and Australia and New Zealand. Most interesting, it is also invasive in a climatic band on the mountain of Mauna Kea in Hawaii. This band shares a similar climate to its native range. By understanding the global distribution of this and other species, it is far easier to predict susceptible environments. This is also true for predicting environments where a species may not be invasive. In California, *Lantana camara* is a widely planted garden ornamental throughout the state, and *Melaleuca quinquenervia* is a common street tree in the southern region of the state. Both species are not problematic in California, yet this book describes their invasion into many other regions of the world or even within other areas of the United States as bearing more harmful consequences. The similarity in the climatic zones where these species have invaded provides insight as to why the drier Mediterranean climate of California restricts their ability to establish. Again, a global perspective becomes critical to predicting the potential invasiveness of a species in other regions of the world, and this book provides that global perspective.

To make better informed decisions on how to prevent potentially harmful introductions, what plants to prioritize, what climatic or environmental characteristics may contribute to the spread and success of invasive plants, and what local, regional, and global policies or legislation are necessary to mitigate against their impacts, I firmly believe it is critical to understand plant invasions on a global level. From my own limited firsthand experiences studying invasive plants outside the United States, I greatly expand my appreciation for the larger picture regarding individual invasive plant species and threatened ecosystems. After reading through the various chapters of this book, I was so impressed by the tremendous amount of valuable information from so many regions of the world. I could not help but wish that such a volume had been available when I was a student or even during my career as a faculty member. This would have been among my most valuable references on invasive plants, and I believe it will be an important book in the personal library of many others.

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March 30, 2021

Joseph M. DiTomaso

Preface

When Charles Elton published his ground-breaking book *The Ecology of Invasions by Animals and Plants* in 1958, he raised the alarm that “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.” Although Elton’s book essentially marked the beginning of the modern field of invasion biology, it took decades for the fledgling discipline to be taken seriously. Even today, there is a movement within academia labelled “invasive species denialism,” arguing that invasion biologists and practitioners tend to exaggerate the harms caused by these species. Meanwhile, regardless of their impacts, these invasions continue at a staggering rate and are truly worldwide in scope as documented in the chapters of this present volume, highlighting global plant invasions.

Given the intrinsic variation in species biology, it is clear that different plant species will vary greatly in their ability to damage and invade various ecosystems, such as natural ecosystems, agroecosystems, or urban environments. Thus, there is a need to carefully assess the impacts of invasive species, avoiding exaggeration but at the same time providing important information on impacts, as detailed in this volume. Even since 1958, much has changed in our relationship with invasive species as globalization and dramatically increased economic growth in certain regions have made the intentional and unintentional transport of invasive species more rampant. Moreover, the specter of global climate change has exacerbated invasion potential, as we have witnessed an accelerated increase in global mean temperature along with other climatic factors that promote the spread of these species. Intrinsically, these species are well-adapted to ride on human coattails and follow us around the globe and thrive where we generate available niches for them. However, this comes at a cost to many sensitive natural ecosystems comprised of plant and animal communities as products of thousands or millions of years of coevolution. Many species have gone extinct as a result of invasive species, and many of these plants have altered ecosystem functions and reduced the value of ecosystem services. Ecosystem services are sometimes difficult to quantify or visualize, but to add to these compromised ecosystem services, there are considerable quantifiable economic costs of invasive species to agriculture, forestry, recreation, urban property values, and other sectors, even impacting iconic cultural landmarks. A full accounting

of these costs also includes the exorbitant expenses in managing these invasive pests year in, year out, as they grow and spread “like weeds.”

This book volume represents a comprehensive overview of global plant invasions in the early twenty-first century. The first few chapters provide an introduction to the nature of plant invasions, defining their scope and impacts, the dynamics of invaded plant communities, global invasion pathways, and the role of global climate change in fostering further plant invasions. From there, experts from every continent and world region highlight the state of invasion in their areas, with chapters covering plant invasions in Asia, Australia, Europe, North America, South America, Central America, Africa, island regions, and mountainous regions. The subsequent three chapters turn to how to respond to the challenge of global plant invasions, examining biotic and economic impacts, advances in management, and the design of global strategies for managing invasive species. In the final chapter, well-known invasion biologist, Daniel Simberloff, addresses the question of whether we are heading to a “future planet of weeds” and what this means for the well-being of our planet and ourselves.

The subject of global plant invasions is very broad and complex, with every world region facing specific issues around particular invasive species. Yet many of the issues are common to many geographic regions, and many invasive plant species have spread via human agency across multiple continents – including lantana, knotweed species, gorse, mile-a-minute weed, water hyacinth, parthenium, prickly pear, ragweed, giant reed, cordgrasses, Siam weed, Himalayan balsam, and mesquite. Thus, there is value in having these global portraits of plant invasions collected in a single volume, provided by expert scientists from across the world who have seen firsthand the impacts and challenges posed by these species. This book provides a comprehensive tool in the hands of undergraduate students and graduate students, invasion biologists from academic and government institutions, nongovernment organizations, policy-makers, and numerous other agencies developing strategies and actions to manage invasive plants on local and global levels. The field of invasion biology is still a young seedling, and this book is full of suggestions for further research and development of this emerging field.

We are very grateful to all the authors for their excellent contributions – it has been a privilege to work with each one of them. We also thank the staff at Springer Nature for their kind support, the external reviewers for providing helpful feedback on the chapter manuscripts, and our families for their encouragement and patience through the long but fruitful process of putting this book together.

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Joseph DiTomaso shows how adventitious roots form to help facilitate rapid spreading of mile-a-minute weed (*Mikania micrantha*) in Yunnan Province, China. Photo credit: David Clements

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Global Plant Invasions on the Rise

1

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Abstract

The data available on the extent of global plant invasion shows a sharp increase in cases and associated costs over the last several decades. Indeed, most of the mixing of the planet's flora due to human agency has occurred in the last 200 years. As in the case of rapidly emerging human pandemics that demand timely action, there have been urgent calls to stem the tide of plant invasions and prevent further spread and associated environmental and socioeconomic impacts. However, the response to most actual and potential plant invasions is far from simple. Naturalized plants have a broad range of impacts, such that a response specific to the particular plant spe-

cies and habitat is often advisable, along with a meaningful dialog among stakeholders. Given the massive scale in changes of the flora in various regions, many naturalized species with minimal impacts are best left alone, whereas other naturalized species that have massive impacts warrant management to prevent further, often irreversible, effects on ecosystems. There exists a considerable array of invasive plants in this category, most of which are truly global, distributed on multiple continents. Of these high-impact invasive plant species, 37 are on the list of the International Union for Conservation of Nature (IUCN) 100 worst invasive alien species. Most of these high-impact species continue to spread in their non-native ranges, including sensitive island and mountain habitats. They also cause a range of socioeconomic impacts on agriculture, forestry, transportation, infrastructure, and cultural values. If current trends in plant invasions continue and are exacerbated by increasing global trade and climate change, many challenges lie ahead. We cannot turn back the clock to recover natural habitats free of invasive plants in most cases, but there are still ways of promoting ecosystem health through reducing populations of high-impact invasive plants and promoting holistic approaches to planet healing.

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Keywords

Biosurveillance · Climate change · Globalization · Invasive plant costs · Island invasions · Planet of weeds · Plant invasion

1.1 Introduction

Many global issues are in ascendance at this point in world history, and there can be little doubt that global plant invasions are on the rise with rates exacerbated by many other forces operating at a global scale, such as climate change and ever-expanding world trade (Meyerson and Mooney 2007; Ziska et al. 2019; Hulme 2021a). Diagne et al. (2021) estimated a worldwide mean annual cost of biological invasions of \$26.8 billion USD between 1970 and 2017, which by 2017 had reached \$162.70 billion USD annually, showing a continual increase with no signs of leveling off. These estimates included the costs of damage due to invasive species and their necessary management, with both likely grossly underestimated due to lack of available data. There are challenges associated in accurately estimating such costs, but more broadly, there is a need for more research on invasive species generally, and invasive plant species specifically, in order to better understand their biology and ecology, as well as their environmental and economic impacts (see Chap 14 for a more detailed assessment). Better-informed international strategies and policies can be developed to tackle this global problem (see Chap 16). In the meantime, it is clear that proactive actions are required immediately to prevent the seemingly inevitable progression towards a “planet of weeds” (Quammen 1998; van Kleunen et al. 2015; Pyšek et al. 2017, 2020; Seebens et al. 2018; Chap 17).

Seebens et al. (2017) analyzed the first reports of species invasions over the past 200 years and found that 37% of these were reported between 1970 and 2014, with no signs of slowing down. Many species in more recent invasions had never been observed to be invasive previously, thus the pool of potential invaders is also on the rise

(Seebens et al. 2018). Seebens et al. (2021) used a modeling approach to predict establishment of naturalized alien invasive species and estimated that, by 2050, their total number would increase globally by 36%. Thus, we can anticipate continual species invasions for the foreseeable future, despite our efforts to stem the tide through the development of better management and surveillance. The pace of globalization is much greater than the efforts to manage invasive species (Seebens et al. 2017; see also Chaps 2 and 16). At the same time, economic costs associated with the damage and management of invasive species are on the rise (Diagne et al. 2021).

Recent pandemics, most notably the SARS-CoV-2 pandemic that emerged in 2020, serve as a strong wake-up call on the extent of globalization and profound risks associated with it. Invasion biologists have made important connections between invasive species and pandemics caused by human pathogens. Vilà et al. (2021) called global pandemics “quintessential biological invasion events” and argued that there is a strong parallel between epidemiology of pandemic organisms and invasion biology, which investigates how species are moved far from their point of origin to various points on the globe via human agency. In many cases the two fields are more directly related, such as when macroscopic invasive species carry pathogenic organisms, increasing human transmission rates (Vilà et al. 2021). Given the close alignment between the two fields, it makes sense to promote sharing of techniques and approaches between them (Ogden et al. 2019). In fact, Hulme (2021b) strongly advocates for a more unified approach to biosurveillance in general, given the risk of failure of more disjointed approaches, as we have seen with respect to both the SARS-CoV-2 pandemic and global species invasions. A growing body of knowledge on invasive plants is available, but the development of worldwide strategies for managing them is still in its infancy, suffering from sizeable gaps between science, management, and policy at various scales (see Chap 16).

In this chapter we provide an overview of the state of the science of plant invasion biology and opportunities to avoid future invasion of plants.

We begin by presenting a brief history of the science, together with outlining the concepts and definitions in the field of invasion biology. This is followed by a geographic overview, mirroring the book chapters that cover various world regions (Chaps 5, 6, 7, 8, 9, 10, 11, 12 and 13). Next, we address the impacts of invasive plants and the challenges associated with measuring these impacts. Finally, we complete the introduction to the status of this crucial field in our time by giving a brief horizon scan of the way forward, with the rest of the story contained in subsequent chapters by other experts in the field.

1.2 Overview of Invasion Biology with a Focus on Plant Invaders: History, Concepts, and Definitions

1.2.1 Brief History of Invasion Biology

The publication of *The Ecology of Invasions by Animals and Plants* by Charles Elton in 1958 marked a clear beginning of the modern field of invasion biology (Davis 2006). Even in 1958, the pace of change due to globalization was seen as promulgating invasion, as Elton (1958) states: “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.” In the book’s preface, he stated that his goals included pulling together three streams: faunal history, ecology, and conservation, with the latter tending to be the overriding theme (Davis 2006). The text was also marked by graphic battlefield examples of invasions, likely inspired by post-war reflections on World War II. It is also important to note that there were invasion biologists who preceded Elton, including Swiss Botanist Thellug (1881–1918) whose work provided the basis for many unifying concepts in the field (Kowarik and Pyšek 2012). Despite Elton’s con-

tribution in the 1950s, the field of invasion biology had limited uptake by researchers until the 1980s, but from then on, citations in the field of invasion ecology increased steadily, outpacing citations of many other traditional ecological topics (Pyšek et al. 2006). Some of this activity was catalyzed by the work of Richard Mack on plant invasions in western North America, focusing on a conservation theme (Mack 1981; Davis 2006). However, it was not until the 1990s that many more scientists participated in the pursuit of invasion biology research, producing a “flood of publications” that continues to this day (Davis 2006; Richardson and Pyšek 2008; Cassini 2020). By the 1990s, policy makers were beginning to comprehend the magnitude of the issue, and when the United Nations Convention on Biological Diversity (CBD) was created at the 1992 Rio Earth Summit, it included provisions for signatories to control or eradicate invasive species (Lindgren 2012). In February 1999, an executive order was signed by the US President calling for action against invasion of alien biological species in the United States, which also set off alarm bells around the world (Clements and Corapi 2005).

In 2008, 50 years after the publication of Elton’s 1958 book, the field of invasion biology had grown considerably, and the book was still the most cited in the field, with 1516 citations by May 2007 (Richardson and Pyšek 2008). Thus, the basic principles set out by Elton have served the discipline well, although the species under consideration and the theoretical underpinnings have radically changed since the book was published (Richardson and Pyšek 2008). As invasive species research and management has continued to grow from 2010 onwards, critiques of the field have also multiplied (Blondel et al. 2014; Van der Wal et al. 2015; Cassini 2020; Davis 2020) along with defenses of the discipline (Richardson and Ricciardi 2013; Rejmánek and Simberloff 2017; Russel and Blackburn 2017; Ricciardi and Ryan 2018). One of the most important concerns regards the very definition of invasive species.

1.2.2 Defining Invasive Plants

Invasive species biology is often criticized for the lack of universal adherence to concepts and principles (Cassini 2020). Because a wide range of plant species may be labeled as “invasive,” it is difficult to generalize. Weed scientists tend to refer to invasive plants as “environmental weeds” to distinguish them from agronomic weeds (Sheppard et al. 2006); however, the two categories are clearly not mutually exclusive because many “environmental weeds” also invade agroecosystems, and vice versa (Thomas and Leeson 2007; Clements 2017). Colautti and MacIsaac (2004) located the following definitions in the literature: a non-native species (Goodwin et al. 1999; Radford and Cousens 2000); a native or non-native species that has colonized natural habitats (Burke and Grime 1996); a widespread non-native species (van Clef and Stiles 2001); and a widespread non-native species that has a negative effect on habitat (Davis and Thompson 2000; Mack et al. 2000). Blondel et al. (2014) argued for a broader definition, referring to the Latin term *in-vadere*, arguing this should be the fundamental element in the development of invasion science, regardless of whether such invasions were human-mediated.

Blackburn et al. (2011) developed a unified framework, representing a “single conceptual model that can be applied to all human-mediated invasions” that is widely used by invasion biologists. The framework includes terms to be applied to species at different invasion stages. “Alien species” are species transported to areas where they are non-native through human agency. Alien species are classed as “casual/introduced” if they are not reproducing in the new environment, referred to as “naturalized/established” if they are able to reproduce, and “invasive” once they demonstrate the ability to spread in the new environment (Blackburn et al. 2011). The division among the three terms “introduced,” “naturalized,” and “invasive” is important, recognizing that many introduced species never become naturalized, and of these relatively few become invasive (Richardson et al. 2000). The difference between the self-sustaining naturalized populations and

invasive populations is somewhat subjective but essentially requires that a species has demonstrated the ability to disperse beyond the site of introduction (Richardson et al. 2000; Blackburn et al. 2011). Legal definitions of invasive species have been developed to support their management by governmental and nongovernmental agencies. The legal definition employed in the 1999 US Executive Order was “an alien (or non-native) species whose introduction does or is likely to cause economic or environmental harm or harm to human health” (Executive Order 13112, 1999). The International Union for Conservation of Nature (IUCN) defined an alien invasive species as a species “which becomes established in natural or semi-natural ecosystems or habitat, is an agent of change, and threatens native biological diversity (IUCN 2000).

When a particular invasive species is highlighted, the big question is often “what impact does it have?” However, impact may be difficult to define precisely. Jeschke et al. (2014) developed seven questions to attempt to unpack invasive species impact:

1. Are only unidirectional changes considered or are bidirectional changes considered?
2. Is the definition as neutral as possible or are human values explicitly included?
3. Is the term *impact* only used if the change caused by a non-native species exceed a certain threshold, or is it used for any change?
4. Are ecological or socioeconomic changes considered, or both?
5. Which spatio-temporal scale is considered?
6. Which taxonomic or functional groups and levels of organization are considered?
7. Consideration of per capita change, population density, and range?

These questions illustrate some of the dilemmas faced by scientists in characterizing invasive species. For example, question 1 demonstrates that some impacts of invasive species on an ecosystem may actually be positive, or both negative and positive. Likewise, question 3 shows that impacts may cover a broad range, and from a management point of view, it may be challenging

to choose at what point should action be taken, especially if the threshold is not clear. The remainder of this chapter, and indeed the rest of the book, provides further input on these important questions.

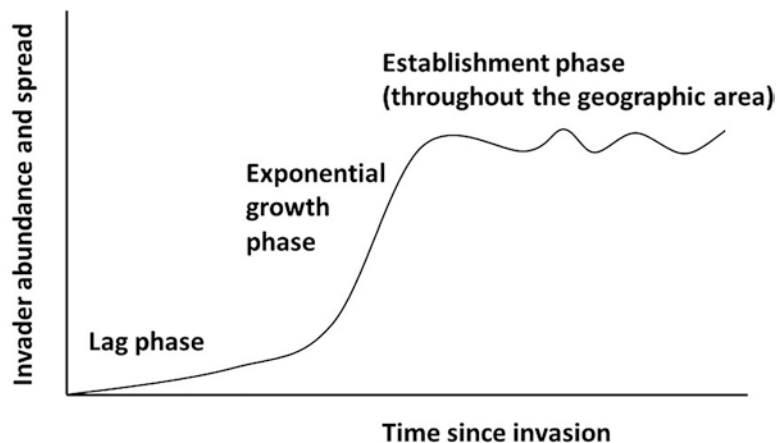
1.2.3 The Plant Invasion Process

Invasion scientists commonly refer to a typical invasion history consisting of three fairly distinct phases: (1) a lag phase after the initial invasion when the invader is relatively uncommon and found in isolated locations, (2) an exponential growth phase when the species rapidly increases both in population size and distribution, and finally (3) a period of time up to the present when the population and distribution have reached their maximum extent, subject to occasional fluctuations due to variation in conditions, including attempts to manage the invasive species (Fig. 1.1). These three phases have also been characterized as introduction, colonization, and naturalization phases (Radosevich et al. 2003). During the lag phase, the invasive species may be difficult to detect and often seen as posing limited risk because of its low abundance. The lag phases of invasions have been documented to range from a few years to centuries in length (Pyšek and Prach 1993; Crooks 2005; Larkin 2012). It is likely that a variety of mechanisms account for the lag phase including dispersal limitations, availability of empty niches, and genetic or phenotypic changes

in the invaded range (Clements and DiTommaso 2011; Espeland 2013; Perkins et al. 2013; Murren et al. 2014). Of course, not all invasions follow the typical trend, and many invasions are not nearly as successful. According to Williamson's (1996) "Tens Rule," only 10% of species entering a dispersal pathway disperse, 10% of these establish in the adventive habitat, and among the species establishing, only 10% become problematic, i.e., the invasive species that follow the pattern in Fig. 1.1.

Several studies have analyzed invasion history in an attempt to predict invasion patterns better, through examining herbarium records and various other forensic ecology methods. Larkin (2012) failed to detect an overriding explanation predicting length of the lag period among several species with periods ranging from 3 to 140 years. Similarly, Flores-Moreno et al. (2015) followed the fate of three invasive plants in the United Kingdom over 200 years and found that these species did not require time to evolve responses to the habitat. By contrast, Fennell et al. (2014) found greater genetic variability in seeds of giant rhubarb (*Gunnera tinctoria*) in Ireland before populations transitioned to the exponential phase. For introduced rangeland plants in the western United States established for periods between 41 and 86 years, Morris et al. (2013) found that while some species followed the usual logistic invasion curve, others showed sporadic crashes and spikes in abundance, likely due to periodic droughts in this relatively arid environment.

Fig. 1.1 Commonly observed trend in the abundance of non-native species invasions over time, illustrating three major phases often recognized in the invasion process



Mosena et al. (2018) computed invasion curves for ten invasive plants in western North America and observed some were logistic while others were more linear. They also computed proportional changes in counties occupied, which allowed them to gain more insight into the geographic spread. For example, the major range expansion period for cheatgrass (*Bromus tectorum*) extended from 1900 to 1950, well beyond the 1900–1930 expansion period emphasized by Mack (1981). Examining the invasion history of 155 tropical grasses invading Australia, van Klinken et al. (2015) showed how 21 of these became widespread and problematic but predicted few new invasions by grass species will occur in Australia.

A key question behind attempts to characterize invasion curves and their history is whether potentially serious invasive species can be detected and dealt with early in the invasion sequence. The potential for eradicating and the cost of eradication is far more favorable in early invasion stages, but it is difficult to predict the seriousness of an invasion early (Daehler 2003; Larkin 2012). In order to attempt to catch potentially serious invaders early in the curve, government agencies and others charged with managing invasive species frequently employ (1) early detection and rapid response (EDRR) and (2) weed risk assessment (WRA).

EDRR advocates argue that from the precautionary principle, virtually all recent or potential invasive species should be assumed to be a serious threat (Westbrooks 2004; Crooks 2005). Given the modest amount of funding available for invasive weed control in California, Funk et al. (2014) pointed out the massive savings from controlling species as early as possible post invasion, and this is all the more true for many other areas around the world where funding is even scarcer. However, because there are so many potential invaders, WRA is a useful tool for prioritizing which invaders are likely to cause the greatest harm. WRA models make use of expert knowledge on potential invasive species, including a variety of measures related to the potential for spread or impact in other geographic areas (Pheloung et al. 1999). However, Hulme (2012)

pointed out that risk assessments are inherently flawed due to the subjectivity of experts and high levels of uncertainty predicting plant invasion dynamics. McGregor et al. (2012) found that the Australian WRA predicted naturalization well but failed to consistently predict the extent of spread. Hulme (2012) recommended augmenting the WRA approach using knowledge of experts to assess uncertainties accompanying weed population and human management dynamics (e.g., interventions to improve ecosystem resilience). More sophisticated approaches to risk assessment are currently under development, e.g., an approach that combines information from knowledge of the invasive plant species and potential recipient ecosystems, utilizing the growing body of knowledge available on both aspects (Probert et al. 2020a). Furthermore, many new invasive species are now emerging, and WRA methods that rely on historical knowledge may no longer be relevant because experts are unaware of risks posed by these new invasive species (Seebens et al. 2018). One useful approach is to look at risks associated with particular taxonomic or functional groups, rather than trying to assess risk across all plant groups. Frameworks have been developed to assess risks associated with various plant groups, such as bamboos (Canavan et al. 2017), Cactaceae (Novoa et al. 2015), and conifers (Richardson and Rejmánek 2004).

Because of the nature of the lag period, managers often fail to realize the high costs of invasions until it is too late (Westbrooks 2004; Mack et al. 2000). A critical question is whether or not impacts can be predicted in advance. Van Klinken et al. (2013, 2015) studied 155 tropical and subtropical grasses in Australia to determine if effects on natural environments, pastures, or agricultural crops could be predicted. Among 155 tropical and subtropical grasses invading Australia, the best predictors of costs were how fast they spread and whether they were semi-aquatic (van Klinken et al. 2013, 2015). The most important invasion pathway for these grasses was through intentional introduction of pasture species to Australia (Van Klinken et al. 2015), a pathway that has contributed to colonization by grass species the world over (Mack et al. 2000;

Morris et al. 2013). Similarly, horticultural introductions, which by definition are intentional, feature prominently among invasion pathways (Reichard and White 2001; Lambdon et al. 2008; Hulme 2009; Barbier et al. 2011). To this day, such pathways are prominent sources of invasion, and increased globalization and commerce tend to exacerbate such invasions.

The study of plant invasion pathways poses the question: How did each of the more than 13,000 naturalized plants throughout the world (Pyšek et al. 2017) arrive at their destinations? Although over the past 500 years many different pathways have been identified, the pathway responsible for more than half of all plant invasions has been deliberate introduction of plants for horticulture and other forms of cultivation (Chap 3). More broadly speaking, the three most important pathways have been introductions for food production, ornamental purposes, and accidental releases (Saul et al. 2017; Pergl et al. 2020). We have witnessed three major waves of plant invasion (di Castri 1989): the age of exploration (1500–1800), the age of industrialization (1800–1950), and the age of globalization (1950 to the present), with each succeeding wave greater than the previous one.

1.2.4 Recent Trends and Drivers of Plant Invasion Including Globalization, Increased Trade, and Climate Change

Many attempts have been made to describe the major drivers of plant invasion. It is tempting to ascribe most of the agency to the invasive plants themselves, because they indeed possess many remarkable qualities, and most invasive plant researchers have a great deal of respect for their subjects, even if the ultimate aim of the research is to control or eradicate these species. However, it is clear that in many cases, the invasive plants should be seen more as the passengers rather than the drivers of the invasion process (MacDougall and Turkington 2005). In the Garry oak ecosystem studied by MacDougall and Turkington (2005), the invasive grasses benefitted from an

ecosystem already being degraded, through a disturbance regime highly modified from its historical baseline state. Thus, reduced ecosystem resistance was the major factor precipitating change. In other settings, invader fitness could be the major driver, or in still other situations climate dynamics could be key. Young et al. (2017) developed a framework for looking at these three factors: ecosystem resistance, invader fitness, and climate dynamics simultaneously, in order to examine the forces determining how well invasive plants invade communities (see also Chap 2).

Each of the elements in the framework devised by Young et al. (2017) involves a considerable array of dynamic factors, and thus understanding plant invasions, and attempting to develop a better system of predicting them, requires an in-depth examination of all three elements. Although there are numerous studies of the three factors in isolation, there is a need for integrated research involving all three elements of the framework (Young et al. 2017; Chap 2). It is relatively easy to produce a map which predicts areas that are climatically suitable for a particular plant invader, but unless ecosystem resistance is overcome (e.g., via anthropogenic disturbance), the plant will not invade a particular area. By the same token, models that predict expanding ranges of invasive plants under climate change may underestimate the extent of invasion for invasive species that evolve in response to changing conditions along the invasion edge, thus increasing invader fitness (Clements and DiTommaso 2011). Indeed, numerous recent studies are revealing that invasive plants can evolve relatively rapidly to changing climatic conditions and that this ability represents a major challenge to their management (Ziska et al. 2019; Clements and Jones 2021a, b).

Humanity ignores the critical linkage between invasive species and climate change at its peril (Seebens et al. 2015; Ziska et al. 2019; Chap 4). It is important to recognize the particular impact of climate change on invasive plants due to the interaction between CO₂ levels and photosynthesis, whereby increased CO₂ impacts plants both through potential increases in photosynthesis and global warming (Ziska et al. 2019). It is also

important to understand that many other features of climate change interact with invasive plants, such as more frequent flooding, droughts, storms, fires, and other extreme events (Colleran and Goodall 2015; Wu and Ding 2019; Fraterrigo and Rembelski 2021; Chap 4). Climate changes not only promote greater spread of plant invasions but also reduce our ability to manage them, through reduced efficacy of herbicides and other methods (Ziska 2020; Clements and Jones 2021a), thereby increasing the costs of management (Rhodes and McCarl 2020).

Globalization and increasing world trade are unquestionably driving much of the rise in plant invasions, with global trade synonymous with the movement of invasive species hitchhiking on commerce, or even the subject of commerce in many cases, e.g., the horticultural trade (Hulme 2021b). Effects of globalization on plant invasions have been well documented, particularly for countries like China where the recent increase in economic growth and trade has resulted in widespread introduction and proliferation of invasive plants (Ding et al. 2008; van Kleunen et al. 2015; Horvitz et al. 2017). Direct effects of globalization on the rate of plant introductions via horticultural trade are well supported by the research (Taylor and Irwin 2004; Pyšek et al. 2010; van Kleunen et al. 2018; Guo et al. 2019). Indirect effects of globalization on invasive species issues are more challenging to understand and quantify. The full scope of indirect effects includes the way that growing trade transforms economies, making nations more likely to import invasive species or to create an environment conducive to invasion. Hulme (2021b) argues that these indirect effects have a far greater impact than direct effects. One striking indicator of the overall trend since the nineteenth century is how the increasing percentage of imports of the global GDP closely mirrors the increasing frequency of number of first records of alien species (Hulme 2021b). Furthermore, the relationship between international trade and invasive species is a rapidly moving target, due to labile trading relationships between countries, supply chain disruptions, newly emerging modes of trade (e.g., e-commerce), and, as recently highlighted, pan-

demic influences (Epanchin-Niell et al. 2021). Given how much the rise in the numbers of new invasions is tied to globalization, Meyerson and Mooney (2007) argue for a concomitant globalization of the knowledge of invasive species to help better coordinate international efforts to deal with invasive species.

1.3 The Geography of Plant Invasions

By definition, plant invasions consist of changes in geographic distribution. Earlier research on plant invasion biology focused mostly on Europe and North America. There was also an earlier focus on island ecosystems, as being clearly very vulnerable to invasions (see Chap 12). Increasingly, however, many invasive plants have become more global, with many species distributions now spanning several continents, highlighting the need for a coordinated global approach to their management (Hulme 2021b; Chap16). There are 11 invasive plants present in at least 35% of world regions within their invaded range, with the most widely distributed species being common sowthistle (*Sonchus oleraceus*) (Pyšek et al. 2017). In terms of invasive ranking within regions, lantana (*Lantana camara*) is at the top of the list, occurring in 120 out of 349 regions with data on invasive status (Pyšek et al. 2017), with 4 other species [apple of Sodom (*Calotropis procera*), common water hyacinth (*Eichhornia crassipes*), common sowthistle, and leucaena (*Leucaena leucocephala*)] having invasive status in over 100 regions (Pyšek et al. 2017).

1.3.1 The Invasion State of the World's Continents

Prior to intercontinental introductions of plants by humans, particularly before the first major invasion wave in the age of exploration beginning in 1500, the flora of each continent was relatively unique, producing co-evolved plant communities specific to various natural ecosystems. Agroecosystems have featured a more universal

flora, dating back to times when crop species were subject to long-distance introductions. Crops were moved along with a complement of agricultural weeds, many of which are among the most widespread organisms on earth (Harlan and de Wet 1965; Krähler 2016). The more recent invasion by non-native plants on a global scale has gone far beyond agriculture. These introductions include some serious agronomic weeds as well as numerous plants that impact natural areas, urban habitats, recreation, and even cultural monuments in their invasive ranges. Many of these invasive plants [e.g., common ragweed (*Ambrosia artemisiifolia*) and mile-a-minute (*Mikania micrantha*)] affect both agricultural and non-agricultural environments (Bassett and Crompton 1975; Day et al. 2016).

Asia, the world's largest continent occupying 30% of the world's surface, represents a broad target for invading plants. In recent decades, increase in trade by orders of magnitude has provided many opportunities for invasive plants to reach Asian countries and flourish (Chap 5). Increases in global trade have brought numerous tropical or subtropical invasive plants, often originating in Latin America, including many notorious invaders such as Crofton weed (*Ageratina adenophora*), Siam weed (*Chromolaena odorata*), lantana, leucaena, mile-a-minute, giant sensitive plant (*Mimosa diplotricha*), parthenium weed (*Parthenium hysterophorus*), and common water hyacinth (*Eichhornia crassipes*). Many of these invasive plants are problematic in other tropical or subtropical areas, such as Australia, Africa, or the Pacific Islands. Common water hyacinth is native to South America and found in all the continents except Antarctica, infesting waterways, disrupting human activities, and denigrating ecosystem services (Coetzee et al. 2017). Although hundreds of non-native vascular plant species are listed as naturalized in Asia, the numbers are relatively low compared to Western Europe and North America (van Kleunen et al. 2015). For many Asian countries, very little data is available on naturalized species. Given human population growth and growth of commerce in Asia, numbers of naturalized species are bound to increase (Seebens et al. 2015; Chap 5). Because

Asian countries vary greatly in their ability to track and manage invasive species, there is an urgent need for better coordination of efforts across the continent (Clements et al. 2019; Chap 5).

In contrast to Asia, Australia ranks as the world's smallest continent. Its invasion history is also very different from the other continents because Europeans only arrived and began introducing non-native species 230 years ago (Chap 6). These introductions have had profound effects on the very unique flora and fauna that were products of millions of years of evolution over the time when Australia was isolated from other land masses. By 2017, nearly 30,000 alien plant species had been introduced to Australia, of which 3027 were reported as naturalized (Randall 2017; Chap 6). This tidal wave of invasive plants over the past several hundred years have had a substantial impact on the native flora and fauna, with particular invasive plants such as cactuses (not native to Australia) having become "text-book examples" of plant invasions. Prickly pear (*Opuntia inermis* and *O. stricta*) infestation reached 24 M hectares at its peak in Australia, with densities reaching 16,000 plants per hectare and seriously impeding livestock production (Dodd 1940). Mass releases of the cactoblastis moth (*Cactoblastis cactorum*) native to South America in 1926 were eventually successful in their management (Dodd 1940). Many cactus species however still impact habitats throughout the continent to this day (Novoa et al. 2015). Reflecting Australia's status as a developed nation, considerable resources have been deployed to manage invasive plants, often utilizing the best available technology (Chap 6). Australia thus provides many useful examples to the rest of the world, often in devising ways to manage some of the world's worst invasive plants [e.g., lantana, kochia (*Bassia scoparia*), Paterson's curse (*Echium plantagineum*), and many others], including innovative biosecurity measures to prevent importation of plant species that are likely to be highly invasive.

Although, formerly, Europe was thought of as more of a source than a receiver of invasive plants, particularly since the majority of invasive

plants in North America originated in Europe (see Chap 8), it has recently become clear that Europe is impacted by a considerable array of invasive plants (Chytrý et al. 2008; Pyšek and Hulme 2011; Rumlerová et al. 2016; Nentwig et al. 2018; Chap 7). Seebens et al. (2021) have predicted that Europe would see the most new naturalized alien invasive species among the continents by 2050. Via the Global Naturalized Alien Flora (GloNAF) database (van Kleunen et al. 2019), Pyšek et al. (Chap 7) showed that of the 4139 naturalized species, the majority originated from other parts of Europe and there are 1926 species that arrived from other continents, mostly temperate Asia. Invasive plants introduced from North America are causing the same kinds of negative impacts over a broad range of habitats, as has been seen in European introductions to North America. The four top-ranking invasive species with the greatest potential impacts in Europe were silver wattle (*Acacia dealbata*), lantana, kudzu (*Pueraria lobata*), and common water hyacinth (*Eichhornia crassipes*) as ranked by Pyšek et al. (Chap 7). These species also have also serious impacts elsewhere in the world.

Among all the continents, North America boasts the highest number of naturalized plants, a whopping 5958 species (van Kleunen et al. 2015; Pyšek et al. 2017; Seebens et al. 2021; Chap 8). Although these species have been arriving for centuries since the time of European colonization, a rapid increase in plant invasion through various pathways such as horticulture, the aquarium trade, and agricultural contamination has occurred in the past 35 years. Within North America, levels of naturalization vary. California, one of the most invaded world floras with 1753 invasive plant species, has the dubious distinction of being “the world’s richest region in terms of naturalized alien vascular plants” (Pyšek et al. 2017). By contrast, Arctic regions in Canada exhibit relatively low levels of plant invasions. As seen in the world at large, the abundance and diversity of invasive plants areas are often linked to higher economic activity. Climate also plays a significant role in this regard. The North American continent features a variety of climate types, some of which are more favorable to plant inva-

sion. Despite relatively intense efforts to manage invasive plants, there are many significant invasive plants in North America [e.g., knotweeds (*Reynoutria* spp.), kudzu, yellow starthistle (*Centaurea solstitialis*), cheatgrass (*Bromus tectorum*), ventenata (*Ventenata dubia*), wild oat (*Avena fatua*), and kochia] that are still increasing in terms of distribution and/or abundance and may increase further with climate change (Clements et al. 2016; Smith et al. 2018; Becerra et al. 2020; Chen et al. 2020; Harron et al. 2020; Harvey et al. 2020).

There are 9905 naturalized vascular plant species recorded in the New World compared to 7923 species in the Old World (Pyšek et al. 2017). South America has at least 2677 known naturalized non-native plants (van Kleunen et al. 2015; Pyšek et al. 2019; Chap 9). It also exhibits high levels of biodiversity, including the highest number of plant species compared to all other continents, and international biodiversity hot spots such as the Amazon rainforest that may be very sensitive to the impacts of plant invasions. Although from the limited research on the extent of invasive species and their relationship to the diverse various habitats in the continent it is clear that invasive species may have serious effects on South American ecosystems, more work is needed to better understand the extent of these effects (Chacón et al. 2009; Herrera and Nassar 2009; Jäger et al. 2013; Zenni 2015; Valduga et al. 2016; Sandoya et al. 2017; Dechoum et al. 2018; Gantchoff et al. 2018; Baruch et al. 2019; Heringer et al. 2019; Chap 9). Central America has fewer known naturalized plant species than South America; yet the total estimated at 1628 non-native plant taxa is substantial (Chap 10). The diversity of regions within Central America is evident in that only 3.9% of the invasive plant species are common to all Central American countries. As with South America, while there are some studies quantifying naturalized invaders in various Central American countries, more research is needed to better understand their impacts (Christenhusz and Toivonen 2008; Chacón-Madriral 2009; Lopez 2012; Bonnett et al. 2014; Daniel and Rodríguez 2016; Chap 10). European colonizers brought non-native

plant species both as crops and hitchhikers to Central America. This along with habitat modifications (e.g., the transformation of landscapes by cash crops) has made some of the most biodiverse habitats on earth vulnerable to invasive species which have continued to arrive in recent decades due to trade and globalization.

Africa, the second largest continent in both area and population, attracts its fair share of plant invasions, with 1139 naturalized plant species in South Africa alone. Other African countries, however, have considerably fewer recorded invasions (e.g., 50 or fewer naturalized plant species for Djibouti, Gambia, Malawi, and Niger (Pyšek et al. 2017; van Kleunen et al. 2019; Chap 11). As with other less technologically developed regions, the non-naturalized flora is not very well studied in poorer African countries. As a result, the number of naturalized species is likely to be underestimated for these countries, and there is a need for more systematic surveys. South Africa, which also has a greater number of problematic invaders, is the only African country that has consistently delivered systematic and well-funded approaches to invasive species management (van Wilgen et al. 2020). Among the numerous naturalized plants in Africa, there are at least 20 naturalized plant species that clearly earn the title as “transformer species” (Richardson et al. 2000), transforming natural vegetation over a considerable swath of Africa (Chap 11). While many of these transformers [e.g., such as lantana (*Lantana camara*), common water hyacinth (*Eichhornia crassipes*), prickly pear (*Opuntia stricta*), giant sensitive plant (*Mimosa pigra*), leucaena (*Leucaena leucocephala*), and parthenium weed (*Parthenium hysterophorus*)] have already been mentioned to be present in other continents, some species are more uniquely an issue for African ecosystems (e.g., several species of *Acacia* from Australia). With so many species that have transformative impacts on African ecosystems, the potential for the spread of new species, and varying abilities of countries in the continent to deal with these plant invasions, a more coordinated approach is necessary. Because the livelihoods of so many in the continent directly depend on the land, invasive species can have devastating

impacts on communities. For example, Pratt et al. (2017) demonstrated that annual costs associated with parthenium weed amounted to \$50-80 million US dollars for African smallholders producing maize in Ethiopia, Kenya, Tanzania, and Uganda.

1.3.2 Are some Areas Particularly Vulnerable to Invasions?

As mentioned with respect to continents like South America, biodiversity hot spots are of great concern with respect to ecological impacts of invasive species. Areas with unique habitats and high levels of endemism such as Oceanic islands (Chap 12) or mountains (Chap 13) tend to be highly vulnerable to invasions. In addition to mountains, there are other terrestrial habitat “islands” which may contain unique and vulnerable flora and fauna, such as freshwater habitats (Dextrase and Mandrak 2006; Kiruba-Sankar et al. 2018; Bolpagni 2021).

The relatively small percentage of the Earth’s total land area occupied by oceanic islands (less than 5%) belies their contribution to global plant diversity, comprising more than 25% of the world’s plant diversity and home to numerous endemic plants. For example, the Hawaiian native vascular plant flora is more than 90% endemic, comprised largely of plant species found nowhere else in the world (Sakai et al. 2002). At the same time, the precipitous decline in these Hawaiian endemic plants, with many documented extinctions, has been clearly linked to overwhelming numbers of invasive animals and plants since Captain Cook “discovered” the islands in 1778. Thus, the Hawaiian and the numerous other remote islands represent a serious conservation crisis, with a race against time to prevent further erosion of the native species populations and diversity by managing invasive species and other factors contributing to decline such as habitat loss (Chap 12). Because such islands are so remote, the ocean generally represents a relatively impenetrable barrier to invasion, but tourism and other forms of development have broken down this barrier in many cases

(e.g., Hawai'i, Fiji, Caribbean Islands, and other popular tourist destinations). Thus, the normally very slow rate of arrival of new species to islands and associated gradual evolution of island flora and fauna over long expanses of time has been disrupted by extremely rapid transport of new species in the modern age (Sax and Gaines 2008; van Kleunen et al. 2015; Dawson et al. 2017; Pyšek et al. 2017; Chap 12).

It is not only the rate of change that is of concern but also the types of plants that are becoming naturalized on islands, creating a very different flora with a completely different array of plant traits. Island floras are generally disharmonic by comparison to mainland floras, meaning they contain a unique complement of plants with certain traits or are limited with respect to taxonomic groupings. Naturalized plants, by contrast, will reflect more on the purposes for which the plants were brought by humans (Hulme et al. 2008; Weigelt et al. 2015) and ultimately come to represent more the world's phylogenetic plant species composition than the unique island species profile (Chap 12). More often though it is largely a single (or relatively few) invasive plant species that overruns island habitats. Ceylon raspberry (*Rubus niveus*) has infested 100 of the 585 km² comprising the island of Santiago in the Galapagos (Renteria et al. 2012). The price tag for eliminating it is about \$10 million USD. Miconia (*Miconia calvescens*) overran large areas of Tahiti (Meyer and Florence 1996) and similarly threatens large areas of the Hawaiian Islands, with costs for control amounting to millions of dollars over the past several decades (Burnett et al. 2007; Leary et al. 2014). Still the isolation of oceanic islands presents unique opportunities to develop sophisticated biosecurity systems to prevent further invasions. In many ways, island biosecurity and management efforts have provided the best examples for the world to follow. Island systems such as the Hawaiian Islands or New Zealand have generated a plethora of research findings and ideas on managing invasive species more proactively and strategically (Daehler et al. 2004; Hulme 2020).

The ecology of mountain invasions resembles island invasion ecology in a variety of ways, as

mountains represent habitat islands in the mainland seas they rise above. Mountains tend to be more inaccessible to human habitation and thus have often been subject to low levels of anthropogenic impacts by comparison to other habitats (McDougall et al. 2011; Lembrechts et al. 2017). Unfortunately, human interference in mountain ecosystems is growing due to climate change, land use change, technology, increased trade, and global connectivity, and some of this interference has been manifested as increased levels of invasive species in mountainous regions (Chap 13). Because invasive species, once introduced, can spread on their own, seemingly inaccessible places in human terms, like many mountain landscapes, are not at all immune to invasive species. Seemingly small changes to infrastructure, such as the establishment of roadways in mountains, have been shown as a natural gateway to invasive plants through disturbance effects and dispersal via vehicles (McDougall et al. 2018; Rew et al. 2018). As with oceanic islands, mountain habitats often cover relatively small areas and have unique features, which make them very sensitive to the effects of invasive species. Most management strategies and challenges for invasive plants occurring in mountains are similar to those in other areas, although the remoteness and inaccessibility of mountain landscapes present unique challenges for surveying for and managing mountain invasive plants (Giljohann et al. 2011; McDougall et al. 2018).

1.4 Assessing Invasive Plant Impacts

1.4.1 Social, Economic, and Environmental Impacts

Assessment of the impacts of invasive species has often been described as one of the weakest links in the field of invasion science (Hulme et al. 2013). Sometimes this is due to a lack of concrete evidence to support the assumption of their damaging effects (Hager and McCoy 1998; Lavoie 2010; Vilà et al. 2011; Epanchin-Niell 2017; Diagne et al. 2021; Chap 14). Advocates attempt-

ing to lobby for resources needed to manage invasive species may be challenged to come up with a clear message in the absence of good data on impacts. It is true that information available on social, environmental, and economic impacts of invasive plants is relatively scarce and there is a need for better assessment of these impacts (Chap 14). However, through the innovative development of new databases like InvaCost and various other efforts to quantify impacts, agencies and researchers are endeavoring to better assess the cost of invasive species to the economy, ecosystems, and society (Blackburn et al. 2014; Hawkins et al. 2015; Pyšek et al. 2017; Bacher et al. 2018; Diagne et al. 2020, 2021; Chap 14).

Innovative methodology and approaches to measure and better assess biotic impacts are being developed (Probert et al. 2020b). The biology and ecology of most major invasive plant species is relatively well known (e.g., Adkins and Shabbir 2014; Day et al. 2016; Gillies et al. 2016; Coetzee et al. 2017; Anderson 2019). However, we are just beginning to understand these species in enough depth to quantify their biotic impacts and design appropriate management measures, including consideration of their impacts on endangered species (Bellard et al. 2016, 2017; Foxcroft et al. 2017; Blackburn et al. 2019; Duenas et al. 2021; Chap 14). Recently, efforts have been made to develop a better classification system for invasive species, to rank them according to either socioeconomic or environmental impacts, in order to develop a more objective assessment for the purposes of research and management (Blackburn et al. 2014; Hawkins et al. 2015; Bacher et al. 2018; Probert et al. 2020b). Moreover, the issues extend beyond scientific understanding. Various stakeholders frame invasive species management very differently depending on their respective values, reflecting a critical need for the development of better ways to engage stakeholders to hear all points of view and communicate the science more honestly and effectively (Courchamp et al. 2017; Novoa et al. 2018). It is also important to recognize that the human side of the management of invasive species generally involves a complex “ecology” of

its own, i.e., “social-ecological systems” (Hui and Richardson 2017; Shackleton et al. 2019). These systems may best be seen as “complex adaptive systems” consisting of many moving parts, so that management is more than just asking: “What does the science say?” Rather, management needs to consider a more holistic, socioeconomic response to invasion, respecting the values of various agencies, special interest groups, and other stakeholders, which together make up an evolving complex system (Hui and Richardson 2017).

One of the most important questions for many of these stakeholders is: “Are invasive plants really that bad?”

1.4.2 Are Invasive Plants Really that Bad?

The two extreme views on impacts of non-native plants are “innocent until proven guilty” and “guilty until proven innocent.” Both scientists and practitioners, and for that matter, the general public, may hold either view or adhere to a position somewhere in the middle of the two extremes (Courchamp et al. 2017; Novoa et al. 2018; Cassini 2020). The position a given person holds may depend on attributes of a particular invasive species, and hence the value of a system of classifying non-native species according to socioeconomic or environmental impacts, although biases may still arise in the classification process (Probert et al. 2020b). Although acknowledging that the impacts of invasive species may be difficult to assess and quantify, Simberloff et al. (2013) maintained that regardless of impact, non-native origin of a species is an important consideration, because frequently non-native species exhibit a lag in their impacts and/or may be having socioeconomic or environmental impacts that are undetected. By contrast, other scientists have insisted that the degree of impact should be part of the definition of an invasive species, with low or no impact species should be classed as benign (Davis and Thompson 2001; Davis et al. 2011). The quest for a more realistic assessment comes partly from a critical examination of invasive spe-

cies biology, often coming from those who believe non-native species are innocent until proven guilty. This critical examination has sometimes been referred to as “invasive species denialism” (Ricciardi and Ryan 2018). Since the 1990s, coinciding with the growth of the field of invasive biology, scientific articles, books, and the popular press have been increasingly questioning the warnings by invasion biologists (Richardson and Ricciardi 2013). This in turn is viewed by some as a threat to the good work done by researchers and practitioners in the field (Russell and Blackburn 2017; Ricciardi and Ryan 2018) while to others a healthy dose of realism serving to refine the science of invasion biology (Sagoff 2018; Munro et al. 2019; Davis 2020). Courchamp et al. (2017) provide some helpful guidelines for potentially resolving some of the issues in invasion biology, including utilizing a dialog model for knowledge mobilization in place of a deficit model that assumes that greater exposure to the science from experts will eventually convince members of society that the experts are right. The dialog model provides for two-way discussions among scientists, government, trade and industry stakeholders, and the general public to address challenging issues such as how best to classify a species as invasive.

How non-native species are classified has implications for their management. If they are considered “guilty until proven innocent,” more immediate attention will be given to recent arrivals, with more active management recommended for species labeled as invasive. Such a universal stance over invasive status has been critiqued as a knee-jerk reaction to a species being “non-native” or “alien,” potentially leading to inappropriate attitudes or management actions towards a given species just because it is non-native, which may even result in harm to the ecosystem (Zavaleta et al. 2001; Bergstrom et al. 2009). There is a growing body of data on how bad invasive plants are, such as the meta-analysis by Kuebbing and Nuñez (2018) looking at plant interactions between 274 vascular plants in 21 habitats, finding that the negative effect of non-native neighbors was twice as bad for natives than for non-natives. In defense of the validity of the

result, Kuebbing and Nuñez (2018) pointed out that although there is disagreement on the incorporation of impact into the definition of invasiveness, it has been shown how impacts increase with increased spread and populations (Simberloff et al. 2013; Hulme et al. 2013). Indeed there is evidence that much of the perceived uncertainty in assessments of invasive species impacts is misguided (Hulme et al. 2015; Wilson et al. 2016; Pauchard et al. 2018; Courchamp et al. 2020).

The application of a classification system based on a scientific assessment of risk or impact (McGregor et al. 2012; Probert et al. 2020b) may result in a more nuanced response based on “how bad” the invasive plant is likely to be in the invaded range. Two unified schemes have been developed to evaluate impacts, utilizing information from the literature and other relevant sources on either environmental (Blackburn et al. 2014; Hawkins et al. 2015) or socioeconomic impacts (Bacher et al. 2018), both featuring five levels of impact: minimal, minor, moderate, major and massive (Table 1.1). The environmental impacts are rooted in the mechanisms used by the International Union for Conservation of Nature (IUCN) Global Invasive Species Database to evaluate invasive species impacts (Blackburn et al. 2014), while the socioeconomic impacts are based primarily on assessments of how the well-being of people is affected by the invasive species (Pejchar and Mooney 2009; Bacher et al. 2018). Clearly, the magnitude of environmental and socioeconomic impact will not always match for a given species, but information from both types of analysis is useful in formulating management approaches (Bacher et al. 2018).

“Massive,” the highest level in these impact assessments, involving irreversible environmental and/or socioeconomic impacts (Table 1.1) may be difficult to appreciate without reference to actual examples. Some good examples of truly massive impacts of invasive plants are found among the 37 plant species selected as part of the list of the 100 worst invasive alien species compiled by the IUCN in 1999 to raise awareness of the risks posed by such species (Lowe et al. 2000; Luque et al. 2014; Table 1.2; Fig. 1.2). Note that this list was never meant to encompass the top

100 worst but rather to communicate that these species are among the worst alien invasive species (Luque et al. 2014). Impacts of the 37 plants on the list range widely but commonly include

Table 1.1 Comparison of the range of impacts of invasive species according to two impact classification schemes: the IUCN Environmental Impact Classification for Alien Taxa (EICAT) (Blackburn et al. 2014; Hawkins et al. 2015) and the Socio-economic Impact Classification of Alien Taxa (SEICAT) (Bacher et al. 2018)

Level of impact	Type of impact assessment	
	Environmental Impact Classification for Alien Taxa (EICAT)	Socio-economic Impact Classification of Alien Taxa (SEICAT)
Minimal	Unlikely to have caused deleterious impacts on the native biota or abiotic environment	No deleterious impacts reported despite availability of relevant studies with regard to its impact on human well-being
Minor	Causes reductions in the fitness of individuals in the native biota but no declines in native population densities	Reductions of well-being can be detected, e.g., income loss, health problems, higher effort, or expenses to participate in activities
Moderate	Causes decline in the population density of native species but no changes to the structure of communities or to the abiotic or biotic composition of communities	Negative effects on well-being leading to changes in activity size, fewer people participating in an activity, partial displacement, abandonment, or switch of activities do not increase human well-being (no increased opportunities due to alien spp.)
Major	Causes the local or population extinction of at least one native species and leads to reversible changes in the structure of communities and the abiotic or biotic composition of ecosystems	Local disappearance of an activity from all or part of the area invaded by the alien taxon; change is likely to be reversible within a decade after removal or control of the alien taxon

(continued)

Table 1.1 (continued)

Level of impact	Type of impact assessment	
	Environmental Impact Classification for Alien Taxa (EICAT)	Socio-economic Impact Classification of Alien Taxa (SEICAT)
Massive	Leads to the replacement and local extinction of native species and produces irreversible changes in the structure of communities and the abiotic or biotic composition of ecosystems	Local disappearance of an activity from all or part of the area invaded by the alien taxon; change is likely to be permanent and irreversible for at least a decade after removal of the alien taxon

impacts on native flora and associated fauna, while many also have impacts on agricultural through similar competitive mechanisms, with many of the species classed as fast growing (Table 1.2). These invasive plants are primarily perennial, with many of them consisting of woody perennials with a tendency to form large patches or thickets that are difficult to manage and may cause irreversible changes to ecosystem functions, consistent with the criteria for massive impacts in the IUCN Environmental Impact Classification for Alien Taxa (Table 1.1). Among them are also some of the worst invasive plants in non-terrestrial habitats, such as common water hyacinth and salvinia (*Salvinia molesta*), with the latter added to the top 100 worst alien invaders list to replace the rinderpest virus that was removed when it was declared to be eradicated globally in 2010 (Luque et al. 2014).

1.5 The Way Forward

For most invasive plants, there is no systematic long-term international strategy like the global campaign mounted to eradicate the bovine rinderpest virus, formerly listed as one of the 100 worst alien invaders by the IUCN (Luque et al. 2014). The eradication effort was ultimately successful after more than a decade of concerted action involving many agencies and a massive

Table 1.2 The 37 plants listed in the International Union for Conservation list of the 100 worst invasive alien species worldwide (Lowe et al. 2000), including the later addition of salvinia (*Salvinia molesta*) (Luque et al. 2014), with impact summaries derived from the ISSG (International Species Specialist Group) Global Invasive Species Database <http://www.iucngisd.org/gisd/> and personal observations of the authors

Common name	Latin name	Impact summary
African tulip tree	<i>Spathodea campanulata</i>	Evergreen tree native to West Africa introduced throughout the tropics, as an invasive threat to native vegetation in many of the Pacific Islands
Black wattle	<i>Acacia mearnsii</i>	Fast-growing nitrogen-fixing tree native to Australia competes reducing native biodiversity in parts of Africa, Eurasia, and the Pacific Islands
Brazilian pepper tree	<i>Schinus terebinthifolius</i>	Evergreen shrub or small tree, native to Brazil, produces deep shade and alters the natural fire regime in numerous oceanic islands
Caulerpa seaweed	<i>Caulerpa taxifolia</i>	Marine alga widely used as a decorative aquarium plant forming dense monocultures excluding most other marine life; cold-tolerant strain, inadvertently introduced into the Mediterranean Sea, spread over more than 13,000 hectares of seabed
Cogon grass	<i>Imperata cylindrica</i>	Native to Asia; considered one of the world's ten worst weeds, has spread to most warm temperate zones worldwide; extensive rhizome system, adaptation to poor soils, drought tolerance, genetic plasticity, and fire adaptability make it a threat to many ecosystems

(continued)

Table 1.2 (continued)

Common name	Latin name	Impact summary
Common cord-grass	<i>Spartina anglica</i>	Perennial salt marsh grass, product of hybridization with European cord-grass; excludes native plant species and degrades wildlife habitat in the invaded range in Europe and New Zealand
Cluster pine	<i>Pinus pinaster</i>	From the Mediterranean Basin, now invades natural shrubland, forest and grassland in many temperate regions, suppressing native plants and altering fire regimes and hydrology
Erect prickly pear	<i>Opuntia stricta</i>	A cactus up to 2 m in height from Central America, considered to be Australia's worst ever weed, also invasive in South Africa
Fire tree	<i>Morella faya</i>	Fast growing, N-fixing tree native to the Azores, Madeira Islands, and the Canary Islands, introduced to Hawaii, New Zealand, and Australia forming dense stands and altering N cycles
Giant reed	<i>Arundo donax</i>	Native to Asia, invades riparian areas worldwide, altering the hydrology, nutrient cycling, and fire regime and displacing native species
Giant salvinia	<i>Salvinia molesta</i>	Floating aquatic fern native to South America that thrives in slow-moving, nutrient-rich, warm freshwater, cultivated by aquarium and pond owners, forming massive, thick mats in wetlands on a massive in its introduced range throughout the world

(continued)

Table 1.2 (continued)

Common name	Latin name	Impact summary
Gorse	<i>Ulex europaeus</i>	A spiny, perennial, evergreen shrub from Europe now established in Mediterranean and subtropical climate zones throughout the world (including North America, New Zealand, Africa, and Asia) displacing cultivated and native plants and altering soil conditions and fire regimes
Hiptage	<i>Hiptage benghalensis</i>	A liana native to southern Asia, invasive in Australian rainforests, Mauritius and Réunion, forming impenetrable thickets and smothering native vegetation
Japanese knotweed	<i>Reynoutria japonica</i>	Herbaceous perennial native to Japan naturalized in Europe and North America found primarily in moist habitats but also in waste places, along roadways and other disturbed areas; hybridizes with <i>R. sachalinensis</i> to form hybrid <i>R. × bohemica</i> which is even more invasive than <i>R. japonica</i>
Kahili ginger	<i>Hedychium gardnerianum</i>	Showy ornamental native to the Himalayas which grows over 2 m tall in wet tropical climates displacing native plants in the parts of Africa, Asia, and on oceanic islands
Koster's curse	<i>Clidemia hirta</i>	Invasive shrub native to the Neotropics, now occurring widely on oceanic islands in the Pacific and Indian oceans invading forest gaps, preventing native plant species from regenerating

(continued)

Table 1.2 (continued)

Common name	Latin name	Impact summary
Kudzu	<i>Pueraria montana</i> var. <i>lobata</i>	Invasive vine native to Southeast Asia, infesting large areas of the southern United States but also naturalized through parts of Europe, Africa, and various oceanic islands, impacting forestry and property values
Lantana	<i>Lantana camara</i>	A significant weed native to central and South America with some 650 varieties distributed in over 60 countries impacting both agriculture and natural ecosystems severely through infesting the forest understory or disturbed areas
Leafy spurge	<i>Euphorbia esula</i>	Herbaceous perennial native to Europe and temperate Asia, now found throughout the world, with the exception of Australia displacing native vegetation and crops through shading and competition
Leucaena	<i>Leucaena leucocephala</i>	Fast-growing, N-fixing tree/shrub native to Central America widely introduced for its beneficial qualities as a forage but is also an aggressive invader in disturbed areas in many tropical and subtropical locations globally
Mesquite	<i>Prosopis glandulosa</i>	A perennial, woody, deciduous shrub or small tree native to Mexico and the southern United States, now introduced throughout the world, particularly invasive in Australia and South Africa, forming impenetrable thickets that compete strongly with native species

(continued)

Table 1.2 (continued)

Common name	Latin name	Impact summary
Miconia	<i>Miconia calvescens</i>	Small tree native to tropical America now considered one of the most destructive invaders in insular tropical rain forest habitats in its introduced range in the Pacific Islands, where it outcompetes native vegetation and increases soil erosion
Mile-a-minute weed	<i>Mikania micrantha</i>	A perennial creeping climber native to central and South America that grows rapidly under optimal conditions competing for light and smothering native plants and crop plants, widespread in its introduced range in southern Asia and the Pacific Islands
Mimosa	<i>Mimosa pigra</i>	Shrub native to central and South America, particularly invasive in parts of South East Asia and Australia, often spreading through natural grassland floodplain ecosystems and pastures, converting them into unproductive scrubland
Privet	<i>Ligustrum robustum</i>	Shrub native to southern Asia, disrupting primary forest regeneration and floral biodiversity in oceanic islands, e.g., Mauritius and Réunion
Pumpwood	<i>Cecropia peltata</i>	Fast-growing tree native to Neotropical regions, rapidly invading disturbed areas, in its invaded range, e.g., Malaysia, Africa, and Pacific Islands

(continued)

Table 1.2 (continued)

Common name	Latin name	Impact summary
Purple loosestrife	<i>Lythrum salicaria</i>	An erect perennial wetland herb native to Eurasia, spreading widely in wetlands in its introduced range in North America, forming monocultures and displacing native vegetation
Quinine tree	<i>Cinchona pubescens</i>	Widely cultivated tropical forest tree native to central and South America but escapes and outcompetes native vegetation in Pacific Islands, e.g., the Galapagos Islands
Shoebutton ardisia	<i>Ardisia elliptica</i>	Fast-growing evergreen tree native to South Asia with fast growth that escapes cultivation especially via frugivory to invade natural areas in its introduced range, e.g., various Pacific islands
Siam weed	<i>Chromolaena odorata</i>	Fast-growing perennial shrub, native to south and Central America introduced into the tropical regions of Asia, Africa, and the Pacific, where it forms dense stands that prevent the establishment of other plant species and is also a nuisance weed in agricultural land and commercial plantations
Strawberry guava	<i>Psidium cattleianum</i>	Thicket-forming tree native to Brazil, naturalized in Florida, Hawai'i, tropical Polynesia, Norfolk Island, and Mauritius having devastating effects on native habitats in Mauritius and Hawai'i

(continued)

Table 1.2 (continued)

Common name	Latin name	Impact summary
Salvinia	<i>Salvinia molesta</i>	Free-floating aquatic fern native to Brazil, it forms dense vegetation mats reducing water flow and negatively affects the biodiversity and abundance of freshwater species
Tamarisk	<i>Tamarix ramosissima</i>	Rampantly invasive shrub native to Asia that may dominate riparian zones of arid climates in North America, South America, Africa, and Australia; depletes water sources, and increases erosion and flood damage, soil salinity, and fire potential
Wakame seaweed	<i>Undaria pinnatifida</i>	Kelp native to Japan where it is cultivated for human consumption, but invades worldwide via fouling ship hulls, now infesting Atlantic, Pacific, and Mediterranean coastal ecosystems
Water hyacinth	<i>Eichhornia crassipes</i>	Aquatic weed originating in South America, now found in more than 50 countries on 5 continents, rapidly infesting and impacting waterways, limiting boat traffic, swimming, and fishing
Wedelia	<i>Sphagneticola trilobata</i>	Mat-forming perennial herb native to Central America and naturalized in many wet tropical areas of the world; readily escapes from gardens and forms a dense ground cover, preventing native species establishment and reduces agricultural yields

(continued)

Table 1.2 (continued)

Common name	Latin name	Impact summary
Yellow Himalayan	<i>Rubus ellipticus</i>	Thorny shrub from southern Asia naturalized in Hawai'i southern United States raspberry and the United Kingdom, forming thick patches and outcompeting native species

program of vaccination and other measures (Morens et al. 2011). Invasive plants are very different organisms than viruses in terms of biology and ecology, and furthermore it is much more difficult to mount a unified, focused effort in most cases because opinions vary on the seriousness of the problem. Nevertheless, progress has been made and strategies are being devised (Pyšek et al. 2020; Chaps 15 and 16). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) is tasked with performing a global assessment, comprehensively examining threats posed by invasive alien species, and making recommendations for policy and management by 2023 (Brondizio et al. 2019; Pyšek et al. 2020).

1.5.1 Techniques and Global Strategies

Members of the general public commonly think about weed control in terms of very basic tools like hand-weeding, using a hoe or a shovel, or perhaps utilizing herbicides. However, far more sophisticated tools and management approaches are now available (Chap 15). In fact, before one even picks up a hoe or some other tool, there are salient management tools that may be deployed in view of the complexities around invasive species. One such tool is “horizon scanning” which strives to look futuristically at “thorny problems”

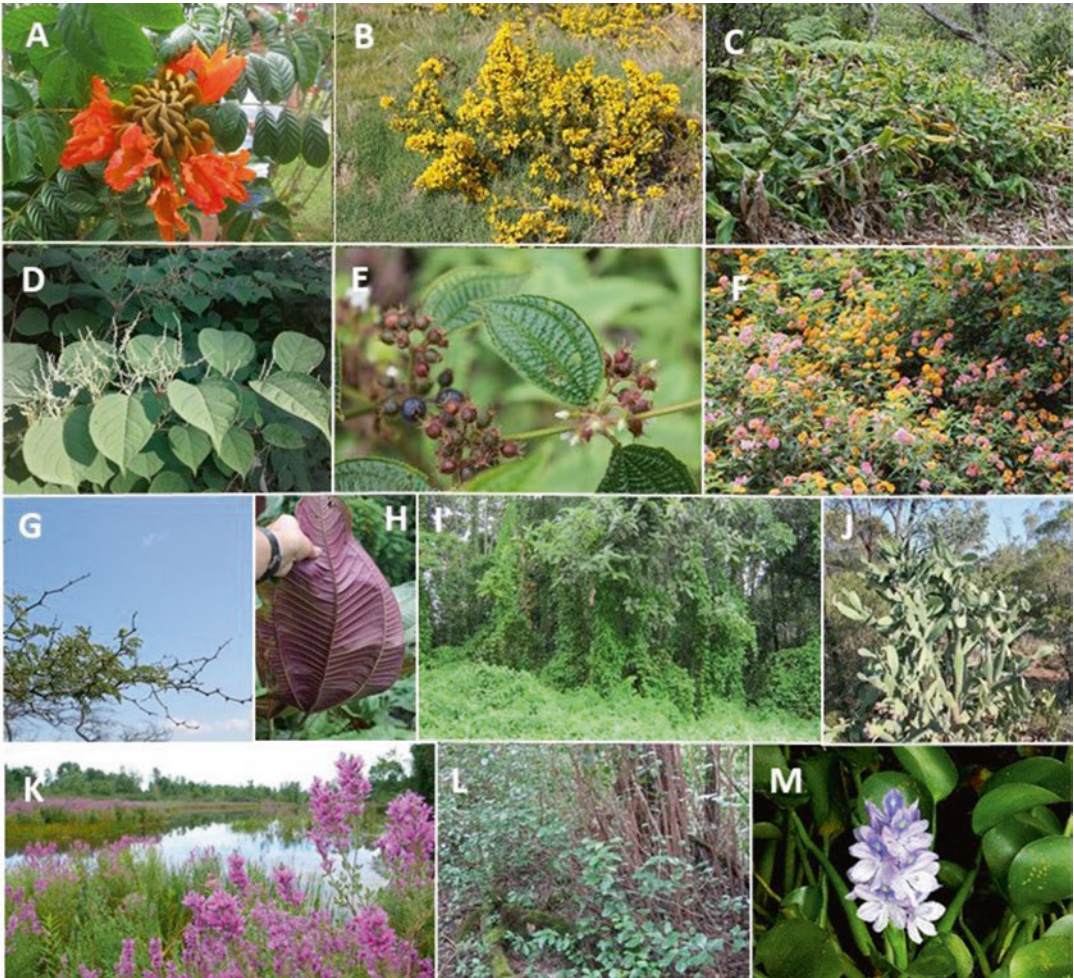


Fig. 1.2 Various invasive plants among the 37 invasive plants in the International Union for Conservation (IUCN) list of the 100 worst invasive alien species worldwide (Lowe et al. 2000). (a) African tulip tree (*Spathodea campanulata*), (b) gorse (*Ulex europaeus*), (c) Kahili ginger (*Hedychium gardnerianum*), (d) knotweed spp. (*Reynoutria* spp.), (e) Koster's curse (*Clidemia hirta*), (f) lantana (*Lantana camara*), (g) mesquite (*Prosopis glan-*

dulosa), (h) miconia (*Miconia calvescens*), (i) mile-a-minute weed (*Mikania micrantha*), (j) prickly pear (*Opuntia* spp.), (k) purple loosestrife (*Lythrum salicaria*), (l) strawberry guava (*Psidium cattleianum*), (m) water hyacinth (*Eichhornia crassipes*). (Photo credits: David Clements (a, b, c, d, e, f, g, h, i, j, l); Srijana Joshi (k); and Anil Shrestha (m))

like invasive plants by brainstorming to account for potential solutions that are not quite available yet, i.e., beyond the current horizon (van Rij 2010; Dehnen-Schmutz et al. 2018). Ricciardi et al. (2017) reported on a horizon-scanning exercise among invasion scientists whereby 14 major emerging issues were identified, including invasive species control using genomic modification, potential impact of Arctic globalization on

Northern Hemisphere invasions, risks surrounding increased pathogenic microbe invasions, and the effects of intercontinental trade agreements.

Many other technical approaches to invasive species management are emerging such as the development of non-invasive cultivars (e.g., varieties that do not produce viable seed) of popular but invasive horticultural plants (Anderson et al. 2006). There are many recent advances in the

technology for monitoring invasive plants, such as environmental DNA (eDNA) technology, remote sensing, or use of drones (Scriver et al. 2015; Vaz et al. 2019; James and Bradshaw 2020). Potent artificial intelligence (AI) is also available to monitor data on invasive plant species through platforms like iNaturalist wielded by citizen scientists. Methods to control weeds in the future might include editing genes via the CRISPR-Cas9 gene drive, as a mechanism either to eradicate invasive plants directly as has been developed for other invasive organisms (Neve 2018; Barrett et al. 2019; Chap 17) or to improve the efficacy of biological control agents (Gurr and You 2016). As well as the developing of cutting-edge technology, efforts are being made to improve older technologies such as applying herbicides ballistically from helicopters to remote areas (Leary et al. 2014), better modeling of invasions (Srivastava et al. 2021), and producing better ecosystem resistance (Seipel et al. 2018).

As seen in the review of many current issues around invasive plant management in this chapter, greater coordination is needed at national, regional, and international levels. Meyerson et al. (Chap 16) make five recommendations towards achieving the goal of effective global strategies: (1) “better tools, indicators, and standards for long-term monitoring of biological invasions and management success at multiple scales”; (2) “better techniques for the evaluation of impacts across different taxa and regions”; (3) “better and additional legislation and normative tools (from global to local contexts)”; (4) “better global biosecurity and biosecurity awareness”; and (5) “increase synergies with other strategies on biodiversity and environmental protection.” Progress is already being made in each of these areas, through a variety of agencies, institutions, and frameworks that have emerged in the last several decades of increasing focus on biological invasions (Chap 16). Still there are critical areas demanding more urgent attention. As part of their scientists’ warning, Pyšek et al. (2020) called for better bridging of local, national, and global measures, prioritizing management interventions based on objective criteria, paying better attention to protected areas, developing better ways of

engaging stakeholders, and developing better species invasion forecasting in the face of global change. Obviously much more needs to be done to avoid a future “planet of weeds” (Quammen 1998).

1.5.2 Opportunities to Avoid a Future Planet of Weeds

The degree to which the earth is becoming a “planet of weeds” depends on where you look. The threat of the homogenization of creation (McKinney and Lockwood 1999; Clements and Corapi 2005) is being realized in habitats like grasslands or wetlands but less so in habitats with greater inherent ecological resistance like forests where long-lived trees tend to delay replacement by non-native species (von Holle et al. 2003; Chap 17). The statistics on numbers of naturalized species tell part of the story, as already reviewed in the current chapter by continent (and Chaps 5, 6, 7, 8, 9, 10 and 11). Thousands of non-native plants have been moved across the globe by humans, intentionally or accidentally, to new niches where they are capable of establishing in the last few hundred years and at an accelerated rate since the sharp increase in globalization beginning in the 1950s (Pyšek et al. 2017; Hulme 2021a, Chap 3). On a finer geographic scale, flowering plants in the Hawaiian Islands provide a cautionary tale. The native flora of the archipelago is well documented, with 1159 taxa approximately 90% endemic, with 9% already extinct. Furthermore, about half of existing native species are rated at various levels of extinction risk, i.e., endangered, vulnerable, or rare (Sakai et al. 2002). There are various reasons for the decline and rarity of the various native species, but clearly the large number of naturalized alien plant species, estimated at 1488 (Pyšek et al. 2017), have played a significant role. Furthermore, non-native animals like wild pigs facilitate dispersal of invasive plants like strawberry guava (*Psidium cattleianum*) while simultaneously reducing native plant populations and spreading diseases like avian malaria (Clements and Corapi 2005). These changes are taking place in the face

of millions of years of evolutionary history of the Hawaiian flora and fauna, often ill-adapted for the recently arrived plants and animals (Sakai et al. 2002). The result is homogenization of flora, such that the average tourist in Hawai'i sees primarily non-native plant species from all over the world, in place of the extremely unique flora of the islands.

By the time it was apparent the flora of Hawaii was being homogenized, it was too late to reverse the trend, as has been the case for most island floras (Mack and Lonsdale 2002), although Herculean efforts have been mounted to attempt to eradicate species like miconia (*Miconia calvescens*) at great cost (Burnett et al. 2007; Leary et al. 2014). Yet perhaps island invasions have an important message for the rest of the world (Clements and Daehler 2007; Chap 12). Like Hawai'i, New Zealand experienced a sharp increase in the influx of invasive plants some 200 years ago, resulting in non-native outnumbering native plant species (Diez et al. 2009). Despite this challenge, New Zealand stands as a prime example of success in dealing with plant invasions, through three proactive measures: (1) national legislation to manage non-native vegetation, (2) a national list of plant species for legal importation, and (3) banning sale and distribution of non-native plants (Hulme 2020). Success has been seen in the population suppression of several invasive plant species through a world-leading biological control program, as well as some eradications of non-native plant species, albeit more due to local efforts than national measures (Hulme 2020). Hulme (2020), in recognizing the somewhat limited success in New Zealand thus far, advocates an outlook that recognizes that success always tends to take longer than anticipated and that successful approaches must account for the values at stake. Similarly, Simberloff (Chap 17) advocates a wholesale change in the relationship between humanity and the biodiversity of natural habitats if we have any hope of avoiding becoming residents of a planet of weeds. Certainly the IPBES assessment process speaks to this need on a global basis (Brondizio et al. 2019). We cannot turn back the clock to recover natural habitats free of invasive

plants in most cases, but there are still ways of promoting ecosystem health through reducing populations of the invasive species with the greatest impacts. There are also many other measures beyond invasive plant management which likewise require a concerted commitment to healing the planet.

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Invasion of Plant Communities

2

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Abstract

Due to numerous human activities, organisms have been transported and either accidentally or deliberately introduced all around the globe. Biological invasions are now considered to be one of the main drivers of global change because many invasive plants have severe ecological, economic, and health consequences. Thus, there is an ever-growing need to better understand invasions to determine how specific plant species are able to establish in communities and, in many cases, expand their range. Here, we describe the invasion process and how it contributes to the invasion of plant communities. We present an invasion-factor framework (IFF) model that uses three factors (climate dynamics, ecosystem resistance, and invader fitness) to explain how each plays a role in the introduction of plants and their ultimate failure or success (i.e., becoming inva-

sive). The invasion of plant communities starts with the uptake of propagules from the native range, followed by their transport to and release into a new territory, where they become established and can spread or expand. Propagule pressure, prior adaptation, anthropogenically induced adaptation to invade, and post-introduction evolution are several theories that have been posed to explain the establishment of invasive plants. Further, traits of invasive plants, either before (existing) or after (developed) introduction, provide a mechanistic understanding with direct ties to the three factors of the IFF. The IFF is a general guide with which to study the invasion process based on specific factors for individual invaders and their target communities. The IFF combines (a) climatic dynamics, analogous to environmental filters; (b) ecosystem resistance, which prevents invasive plants from becoming established even if they are able to overcome the climate factor; and (c) invader fitness, relating to the genetic diversity of invasive plants, which allows them to become established after overcoming climate and ecosystem resistance factors. Case studies from the literature provide examples of research investigating each of the three factors of the IFF, but none exist that describe all the factors at once for any given invasive plant species. The application of the IFF for management is most appropriate once an invasive plant has become established,

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as preventative measures before this point rely only on accurate identification (detection) and removal (response). The IFF model should be considered as a tool to establish research priorities and identify components in the invasion process and inform restoration efforts. We advocate that the IFF should be integrated into management practices to help in the decision-making process that contributes to more effective practices that reduce the occurrence and impacts of invasive plants in a range of communities.

Keywords

Climate factor · Ecosystem resistance factor · Invader fitness factor · Multistep invasion process · Phenotypic trait diversity · Propagule pressure · Spatial scales

2.1 Introduction

In his book entitled *The Ecology of Invasions by Animals and Plants*, Charles Elton (1958) referred to biological invasions as “one of the great historical convulsions in the world’s flora and fauna.” Invasions are now recognized as one of the main drivers of global change (Vitousek et al. 1996; Sala et al. 2000). As a result of various human activities, the number and importance of invasions have only increased in recent times. Through migration, colonization, transport, and international commerce, human activities have moved plants to new regions for hundreds of years, and these events have contributed greatly to the introduction of a range of species around the globe (Mack et al. 2000; Crosby 2003; Bossdorf et al. 2005). Although many naturalized and invasive plants are the product of accidental introduction as contaminants in agricultural products (e.g., seed lots, hay, wool fleeces, etc.) and attached to cargo and machinery, the vast majority of naturalized and invasive plants have been deliberately introduced, either for food, horticultural purposes (i.e., ornamental plants), or medicinal uses (Mack and Lonsdale 2001; Reichard and White 2001; Mack and Erneberg

2002; van Kleunen et al. 2018). Deliberately introduced plants experience benefits not available to accidentally introduced plants, such as protection during transport from the native to the new range, introduction of seeds or propagules in large numbers, introduction at several entry points, and post-introduction protection in a habitat suitable for survival and growth (Novak and Mack 1995; Mack et al. 2000).

As plants become invasive in a new territory, they can have profoundly negative ecological, conservation, economic, and health consequences (D’Antonio and Vitousek 1992; Wilcove et al. 1998; Mooney and Hobbs 2000; Pimentel et al. 2005). Because of their negative impacts, invasive plants have been a focus of scientific research and a source of concern to natural resource managers (Mack et al. 2000). Much of the research has been aimed at predicting which plants will become invasive through identification of traits or characteristics associated with invasiveness (Richardson and Pyšek 2006, 2007; Pyšek et al. 2009; van Kleunen et al. 2010, 2011) and at the identification of the attributes or conditions that make communities susceptible to invasion (Shea and Chesson 2002; Jenkins and Pimm 2003; Rejmanek et al. 2005; Richardson and Pyšek 2006; Didham et al. 2007). Invasive species research has led to the development and testing of numerous ecological and demographic hypotheses (Henneman and Memmott 2001; Blumenthal 2005; Hierro et al. 2005; Jeschke 2014; Lau and Schulties 2015). Beyond providing basic ecological and evolutionary insights (Sax et al. 2005), the research also has value to public and private entities when it can be applied in the management of invasive plants, including restoration (Wittenberg and Cock 2005; Gaertner et al. 2012).

2.1.1 The Multistep Process of Invasion

The invasion of plant communities occurs when organisms are introduced into a new range, where their descendants persist, proliferate, and spread (Mack et al. 2000; Colautti and MacIsaac 2004). The invasion process can be viewed as a series of

steps in which propagules of a species (seeds, eggs, larvae, rhizome and stem fragments, mature individuals, etc.) are taken up from the native range, transported by a vector, released into a new area where they become established, and eventually spread beyond their points of introduction (Fig. 2.1) (Kolar and Lodge 2001; Sakai et al. 2001; Lockwood et al. 2005). However, according to the “tens rule” (Williamson and Fitter 1996), very few plants that are taken up in a native range and transported to a new territory will ever become invasive. That is because there is a high probability of mortality occurring at many points during the journey from a plants’ native range to its introduced range. First, organisms can die during transport, and following their release into a new area, invasive individuals may be extirpated because of climate mismatch (climate dynamics) or ecosystem resistance by native communities (see the Modeling section below). Alternatively, some invasive individuals survive and persist in these new locations and are said to be naturalized (i.e., they become incorporated within the resident community) (Richardson et al. 2000; Novak and Mack 2001). While many plants will remain in the naturalized category, a much smaller fraction of plants will go on to become invasive. At this point, the abundance of invasive plants has increased so that they are now prominent in the new range (and usually become more widespread or expand), and the plants’ negative ecological consequences are amplified, and the economic costs increase (Novak and Mack 2001).

The transition from initial introduction of a plant species to it becoming invasive may occur relatively quickly, but this transition may also require an indefinite length of time (years to decades) (Fig. 2.1). The time delay in the transition to invasiveness is referred to as the **lag phase**. It is during the lag phase that extirpation of invasive populations is most likely to occur (see Application section). Alternatively, variation in the duration of the lag phase may be a result of multiple interacting factors. Mack et al. (2000) provide a detailed discussion of these factors, including (1) demographic lags during which the size of invasive populations increase slowly, (2) environmental and demographic stochasticity

(which may signal the role of climate dynamics and ecosystem resistance), (3) additional introduction events that may occur during the lag phase but go undetected, and (4) the time required for post-introduction evolution to occur, based on invader fitness. If a plant species transitions to become invasive, the lag phase is followed by a period of rapid exponential proliferation in population size, population number, and the areal extent of the plant species in its new range: **rapid range expansion** is underway (Gurevitch et al. 2011). In time, the **saturation phase** occurs, and the geographical limits of an invasive plant species in its new range are realized and the population ceases to expand further (Fig. 2.1).

2.1.2 Native Range Dynamics

While a concatenation of events, including each step in the invasion process, determines whether plant communities are invaded, the first step of every invasion begins with the uptake of propagules from native populations. This means that the amount and distribution of phenotypic trait variability and genetic diversity within and among native populations can contribute to the likelihood of invasion. Therefore, the biogeographic and evolutionary history and ecological and biological characteristics of invasive plants in their native ranges can have a substantial impact on whether, or not, establishment followed by spread or expansion occurs (Novak 2007; Taylor and Keller 2007; Keller and Taylor 2008).

The probability that a plant species will become invasive appears to be influenced by the size of its native geographic range with those more widely distributed, more likely to become invasive (Pyšek et al. 2009; Jenkins and Keller 2011). If plants are broadly distributed in their native range, they have the ability to occupy more ecological habitats because they can tolerate a broader range of climate regimes (Pyšek et al. 2004, 2009). Thus, different populations of widely distributed native plants are more likely to possess prior adaptations that will contribute to fitness (survival and reproduction) and allow

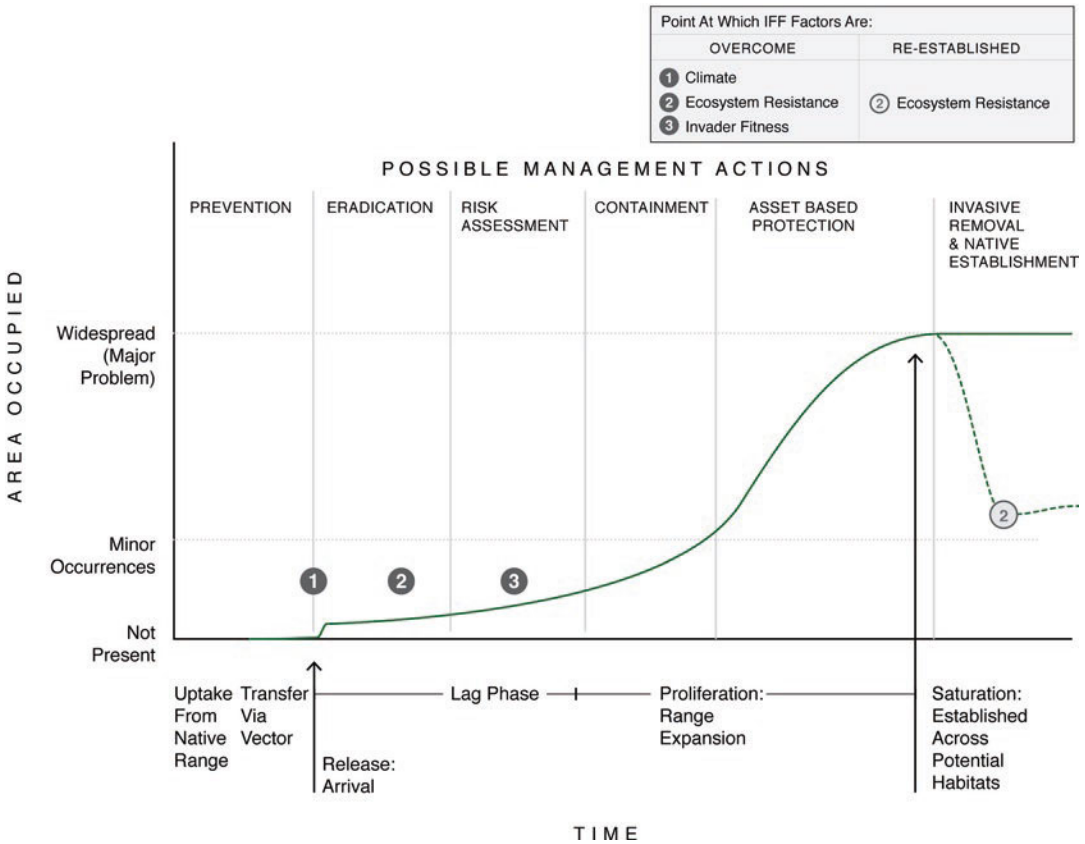


Fig. 2.1 The invasion process, illustrated as the area invaded over time (first x-axis) and possible management actions (second x-axis) that can be implemented depending on the area invaded. The point at which different filters in the invasion-factor framework (IFF) model are over-

come is also included. Once the invasive species has become widespread and saturated across all suitable habitats, it may be possible to decrease the area occupied (dotted green line) by reestablishing one or more of the IFF factors

them to invade plant communities in the introduced range (see the General Theories section). Phenotypic and life history trait diversity (the invader fitness factor in the IFF model) also appear to be correlated with the distribution of plants in their native range: plants with a broad native geographic range size exhibit higher trait diversity (Jenkins and Keller 2011).

2.1.3 General Theories of Plant Community Invasion

The number of studies focused on invasive plants continues to increase as established hypotheses are tested, new hypotheses are proposed, ecologi-

cal theories are applied, and empirical research is conducted (Enders et al. 2020). These theories include propagule pressure, prior adaptation, anthropogenically induced adaptation to invade (AIAI), and post-introduction evolution. They are important to touch on as they provide a basis for our current understanding and future research and are related to the conceptual framework of the IFF model.

Propagule pressure is defined as the number of individuals transported to and introduced into a new range or habitat (introduction effort) (Kolar and Lodge 2001; Lockwood et al. 2005; Simberloff 2009; Ricciardi et al. 2011; Blackburn et al. 2015). With high propagule pressure, invasive plants are buffered from the influence of sto-

chastic events during all phases of the invasion process, and large founder populations and/or multiple introduction events will characterize the release of an invasive plant species in its new range (Simberloff 2009; Novak 2011). Propagule pressure not only holds demographic and ecological consequences for invasive plant introductions; it also has genetic consequences: high propagule pressure (compared to low propagule pressure) will likely increase the overall genetic and phenotypic diversity of populations in their new range, thus decreasing the potential for severe founder effects (Novak and Mack 2005; Simberloff 2009). In addition, high propagule pressure may lead to the formation of introduced populations that contain the genetic information of multiple native populations or admixtures (Kolbe et al. 2007; Novak 2011; van Boheemen et al. 2017). Propagule pressure can also influence the likelihood of invasion through the introduction of individual(s) with prior adaptations for invasiveness or by increasing the potential for post-introduction evolution.

Within evolutionary biology, the term preadaptation describes when a trait that evolved in one environment attains a different function (Futuyma et al. 2005). Rather than preadaptation, we will use the term prior adaptation (*sensu* Hufbauer et al. 2011). Prior adaptations involve the chance sampling of genotypes (and phenotypes) that have evolved in one environment (the native range), with the subsequent release of these genotypes into new environments (the introduced range), where they fortuitously contribute to fitness (i.e., the invasion of plant communities) (Dietz and Edwards 2006; Bossdorf et al. 2008; Hufbauer et al. 2011). Prior adaptation is associated with niche conservatism in invasive plants (Broennimann et al. 2007). Additionally, phenotypic plasticity that occurs among individuals in native populations would represent another form of prior adaptation contributing to invasions (Richards et al. 2006). Thus, invasions are not only influenced by the attributes of plants and communities, but invasions may also be determined by the performance of certain genotypes/phenotypes under specific environmental conditions. Greater propagule pressure increases the

likelihood that individuals with prior adaptations will arrive in areas with the appropriate ecological condition, thus increasing the potential for invasion (although the potential to invade may be population- and location-specific).

Hufbauer et al. (2011) described a specific form of prior adaptation: anthropogenically induced adaptation to invade (AIAI). With this mechanism, prior adaptations may take place through adaptation to human-altered (disturbed) habitats in the native range of a species. Populations with these prior adaptations that arise in human-altered habitats should therefore increase in abundance in other areas disturbed by human activities. In addition, because such areas are frequented by humans, there is increased potential for the uptake and transport of propagules to new ranges. If these propagules are introduced into similar disturbed habitats in the new range, they should have high fitness in the new range. Such a scenario is likely to result in a truncated lag phase that results in a faster transition from introduction to establishment to spread or expansion. Finally, because human alteration of habitats is ongoing and ubiquitous around the globe, AIAI is likely to contribute to increased rates of invasion in the future.

Post-introduction evolution is now widely recognized as an important mechanism contributing to invasion (Lee 2002; Cox 2004; Facon et al. 2006; Novak 2007; Prentis et al. 2008; Colautti and Lau 2015; Estoup et al. 2016) and has been demonstrated in a growing number of studies (e.g., Maron et al. 2004; Blair and Wolfe 2004; Lavergne and Molofsky 2007; Cano et al. 2008; Dlugosch and Parker 2008; Lachmuth et al. 2010; Xu et al. 2010). Post-introduction evolution in the new range of an invasive plant species occurs in association with the following events: generation of admixture populations, outcrossing or hybridization among individuals with different genotypes, genetic reshuffling and/or recombination that can generate novel genotypes and phenotypes, and natural selection on these novel phenotypes [e.g., the evolution of increased competitive ability hypothesis (Blossey and Notzold 1995), see Modeling section]. Clearly, sufficient genetic diversity (especially additive genetic variance)

within introduced populations is a prerequisite for post-introduction adaptive evolution (Lee 2002; Prentis et al. 2008; Estoup et al. 2016). Increased propagule pressure increases the likelihood that high levels of genetic diversity will occur within invasive populations and therefore set the stage for spread or expansion through post-introduction evolution (Novak and Mack 2005). These findings concerning post-introduction evolution suggest that it may be more difficult than previously thought to predict whether an invasion will occur, and its timing, because for different plants this process can require variable amounts of time for different populations, in different habitats.

In addition to these theories, there is a need to develop models or theoretical frameworks for gaining a better understanding of the factors that contribute to the invasion of plant communities. Now we will introduce modeling efforts that describe the factors that create barriers to invasiveness and then provide case studies that illustrate them.

2.2 Modeling Efforts

We introduced invasion using a large-scale, global viewpoint that combines the uptake and transport process (from the native range) with the introduction and establishment process (into the introduced range) of a non-native species. Here, we parse the factors that are contributing specifically to the spread or expansion of invasive plants in target communities. Our focus is on plant traits in relation to the IFF model, which accounts for climate dynamics (climate matching), ecosystem resistance, and invader fitness (genetic factors). These factors may be viewed as similar to the abiotic and biotic filters described in community assembly theory and previously related to niche and invasion theories (Keddy 1992; MacDougall et al. 2009; Fukami 2015).

2.2.1 Invasion Factors and Plant Traits

In order for invasive plants to successfully establish and spread or expand in a resident commu-

nity, they must be well suited to the climate, able to outcompete native plants, and able to successfully increase population size and range across the new region (Theoharides and Dukes 2007; Hellmann et al. 2008). Research into the first necessary factor, climate matching, has noted certain characteristics common to invasive species that enable them to establish and expand in many climates (Jones et al. 2019). Hypotheses regarding the ability of invasive plants to increase population sizes and expand their ranges often focus either on characteristics that are common to invasive plants or on factors that make resident communities more likely to be invaded (Perkins and Nowak 2013). Invasive plants are hypothesized to exhibit fast growth, high seed production, strong dispersal abilities, and low metabolic costs (Blumenthal 2005). Such hypotheses have led to numerous studies comparing traits of invasive plants to co-occurring natives (Grotkopp et al. 2002; Cavaleri and Sack 2010).

Compared to noninvasive plants, invasive plants usually exhibit higher diversity in traits and greater phenotypic values for plant growth characteristics (Leishman et al. 2007; Pyšek and Richardson 2007; van Kleunen et al. 2010, 2011; Godoy et al. 2011; Jenkins and Keller 2011), but these differences can vary by specific traits and environmental context and among plant species (Daehler 2003; Leffler et al. 2014). Invasive plants tend to be positioned more towards the “fast” end of the leaf economic spectrum (Wright et al. 2004), with higher values of traits associated with fast growth (e.g., relative growth rate, specific leaf area, leaf N) than noninvasives in the resident communities that they invade (Baruch and Goldstein 1999; Leishman et al. 2007; Feng et al. 2008). Van Kleunen et al. (2011) conducted a meta-analysis of 125 invasive and 196 noninvasive plants and concluded that the invaders generally had significantly higher (better) values than noninvasive plants for 6 performance-related trait categories: physiology (e.g., photosynthetic rate, transpiration, nitrogen use efficiency, and water-use efficiency), leaf area allocation (e.g., leaf area index, leaf area ratio, and specific leaf area), shoot allocation (e.g., shoot-root ratio), growth rate (e.g., increase in size or biomass over time),

size (e.g., biomass of roots, shoot, and whole plants, plant height, and total leaf area), and fitness (e.g., traits associated with reproductive output, seed germination, and survival). In addition, invasive plants typically exhibit higher levels of phenotypic plasticity, or plastic response, when compared to noninvasive or co-occurring native plants (Daehler 2003; Richards et al. 2006; van Kleunen et al. 2011; Davidson et al. 2011). High levels of phenotypic plasticity allow invasive plants to establish and persist in a wide range of habitats and environmental conditions, especially disturbed sites, which often exhibit high habitat heterogeneity at small spatial scales.

Existing Traits What prevents plants with existing traits (that enable invasion) from becoming highly abundant in their native range? The community in the native range may possess an entirely different suite of trait combinations than what the targeted or resident community has, leading to the evolution of more efficient resource use. In a study comparing traits of long-term native and newly established invasive plants in multiple Mediterranean climate systems, the invader occupied higher slopes in graphical representations of two plant traits in four of the five systems studied, suggesting that invasive plants were more efficient at using resources than the native members of the targeted or resident communities (Funk et al. 2017). Trade-offs, such as a high photosynthetic rate (advantage) offset by low water-use efficiency (disadvantage), may be critical to structuring resident communities and maintaining coexistence (Chesson 2000; Kimball et al. 2013). In some cases, these trade-offs promote rare plant advantages. Studies of trade-offs for high growth rate and stress tolerance indicate that successful invaders appear to have an ability to achieve high values of both types of traits (Kimball et al. 2014b; Valliere 2019). Perhaps trade-offs structure resident communities that slowly assemble over time, and invasive plants come from communities in their native range where higher values of both types of traits have

been favored. Higher growth rates and stress tolerance traits would be a novel combination enabling plants to become invasive in a new range by outcompeting noninvasives (Fig. 2.2).

Developed Traits Another possibility for the successful establishment and expansion of invasive plants is that they develop new traits following introduction, through rapid phenotypic evolution (Stockwell et al. 2003; Xu et al. 2010). Researchers have struggled to understand how newly introduced plants may undergo rapid evolution despite low genetic diversity that often corresponds with invasion, but one possibility is that multiple introductions increase genetic diversity (Lockwood et al. 2005; Novak and Mack 2005; Lavergne and Molofsky 2007). Under this scenario, strong pressure(s) allow for post-introduction selection, even when populations have low genetic diversity (Dlugosch and Parker 2008).

The evolution of increased competitive ability (EICA) hypothesis is based on the idea that invasive plants will experience reduced selection for defensive traits upon occupying a new habitat (introduced range) without their natural enemies (the Enemy Release Hypothesis) and are thus able to invest more in traits that increase their competitive ability, which contributes to invasion (Blossey and Notzold 1995). The development of this hypothesis has led to a flurry of research, yet many studies have not been able to find strong support for EICA, instead only revealing invasives with trait values favoring competitive abilities and no explanation of how the traits evolved (Colautti et al. 2004). This was a similar finding for the Enemy Release Hypothesis (Jeschke et al. 2012), emphasizing the need for studies on traits of the same plants in the native range compared to the introduced range to understand the evolution of traits related to establishment and expansion (Thebaud and Simberloff 2001; Bossdorf et al. 2005).

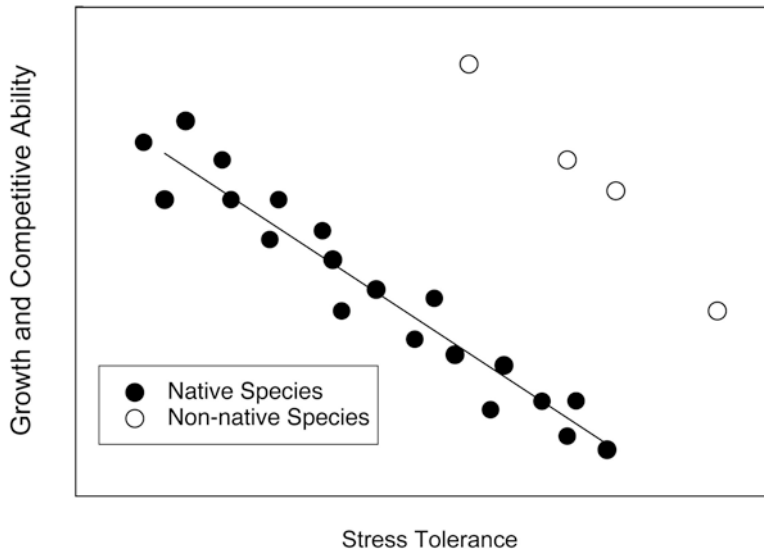


Fig. 2.2 Hypothetical diagram indicating the trait values of native plants (filled circles) and invasive plants (open circles) in a community. Coexistence in the native community is maintained by an among-plants trade-off between traits related to stress tolerance or fast growth. Niche segregation during community assembly should

prevent two plants with the same combination of traits from becoming established, so this community would be resistant to invasion. Invasive plants may be able to invade due to higher values of both traits, indicated by a higher slope on the trade-off plot

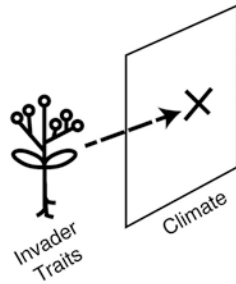
2.2.2 Invasion-Factor Framework Model

Abiotic environmental conditions, the attributes of native ecosystems, and the fitness of invasive plants all determine whether or not plant communities will be invaded (Young et al. 2017). Evaluating the importance of all three factors (climate dynamics, ecosystem resistance, and invader fitness) for any invasive plant can help in better understanding how establishment and expansion have occurred and how to prevent and/or control it in the future. We present a conceptual model, the invasion-factor framework (IFF), which expands on Young et al. (2017), to integrate and evaluate the role and importance of the factors that act to prevent an invasive plants from establishing and expanding in resident communities (Fig. 2.3).

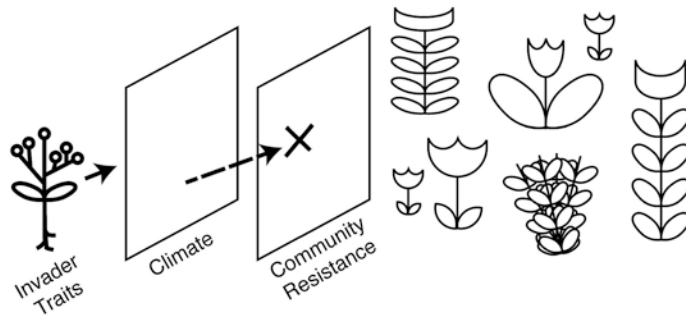
Each factor in the IFF (Fig. 2.3) can be visualized as a static feature that acts sequentially, as this is useful for conceptual purposes. However, we expect these factors to be dynamic, even oper-

ating simultaneously, thus allowing for feedbacks and interactions. For example, climate dynamics may be based on long-term averages for precipitation and temperature, but extreme weather events are likely to lead to greater environmental stochasticity and the association with other climate parameters. Further, the factors of climate dynamics and ecosystem resistance may be more associated for broadly distributed invasive plant generalists making them more likely to be better established than invasive plants with specific characteristics (Pyšek et al. 2009; Saarinen et al. 2019). Ecological niche models have been used to map the potential distribution of invasive plants based on current and future conditions. Such models demonstrate that the range of many invasives are expected to increase with changing climates (Jarnevich et al. 2018). However, an understanding of how climate change has influenced current (and future) invasions requires the incorporation of ecosystem resistance and invader fitness factors into these models (Young et al. 2017).

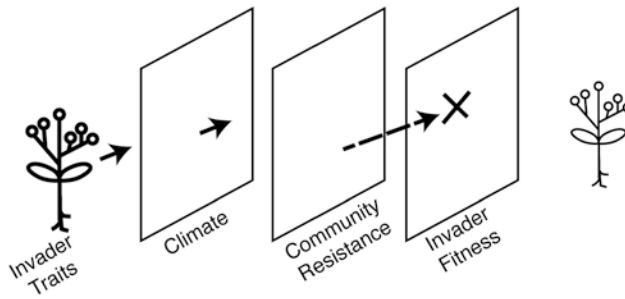
A. Climate mis-match (Invader not able to survive environmental conditions)



B. Resistant community (No vacant niches or invader niche filled)



C. Low invader fitness (Lack of genetic variation, low plasticity, etc.)



D. Invasion (All three factors overcome)

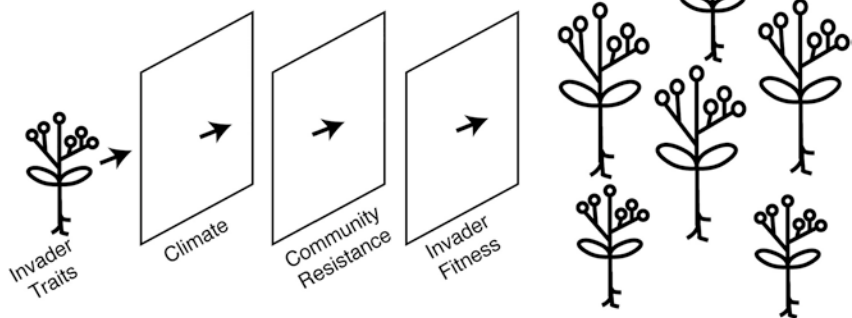


Fig. 2.3 Conceptual diagram indicating potential filters or barriers to the success of invasive plants following dispersal to novel habitats. (a) Traits of invasives interact with climate conditions to determine whether the plants will be able to survive (climate factor). (b) Composition and functional traits of the existing biotic community interact with traits of the invasive plants to determine

whether the plants will become invasive (ecosystem resistance factor). (c) Plasticity of invader traits, the number of dispersal events, resulting genetic diversity of the invader population, and the ability to adapt to changing climate and biotic conditions determine invader fitness. (d) If all filters are successfully overcome, then the plants will become invasive

Climate Dynamics The climate factor (Fig. 2.3a) is analogous to an environmental filter that prevents non-native or introduced plants with traits not well suited to the new environmental conditions from establishing. Many invasive plants are generalists and can withstand a wide range of environmental conditions (Qian and Ricklefs 2006). Traits that allow for high growth rates may enable plants to be successful in resident communities that experience disturbance(s) and nutrient addition (Blumenthal 2006). Disturbances that lead to reduced or complete removal of vegetation create vacant niches that often favor invasive plants. Ruderal types are the most frequent and can quickly occupy these open spaces, thus altering the environmental conditions through priority effects (Hess et al. 2019). The anthropogenically induced adaptation to invade (AIAI) hypothesis, introduced in the previous section, suggests that plants adapted to human-disturbed habitats are able to easily colonize new locations across the globe as humans disturb and homogenize them (Hufbauer et al. 2011). Invasive plant trait values determine resource use under different environmental conditions; thus the traits, in combination with climate dynamics, can be used to help explain their ability to establish and (potentially) expand.

An additional stress for resident plant communities is climate change, which can hasten and in some cases cause composition and structure alterations, making them more vulnerable to invasion. A continuous disturbance, such as drought-induced mortality of native plants, will reduce ecosystem resistance and create vacant niches to be filled by invasives (Kimball et al. 2014a). An increase in fire frequency that is related to climate change can promote “fire-adapted” invasive plants (Garcia-Duro et al. 2019). Cheatgrass (*Bromus tectorum*), an introduced annual grass in western North America, invades post-fire and increases the frequency of fires through positive feedback mechanisms, such as early phenology and increased fuel loads and connectivity. These mechanisms along with an annual life cycle favor cheatgrass in extreme drought and fire-prone conditions and ultimately

lead to further expansion and prevention of native recovery (D’Antonio and Vitousek 1992; Mack et al. 2000; Brooks 2003).

The availability of abiotic resources influences the climate factor, such that ecosystems with limited resources tend to be less invaded than those with high resource levels (Colautti et al. 2006). Atmospheric N and other anthropogenic disturbances have added to soil nutrients, which frequently lead to increases in the abundance of invasive plants (Brooks 2003; Kimball et al. 2014a). Valliere (2019) found that native plants exhibited increased growth when grown alone with higher levels of N and water but were quickly outcompeted under high resource conditions when grown with invasive plants. The fluctuating resource theory predicts that invasion of resident communities increases with greater amounts of unused resources (Davis et al. 2000). The theory incorporates increases in available resources due to disturbances that either decrease resource use by native plants or increase abiotic resources.

Ecosystem Resistance The ecosystem resistance factor (Fig. 2.3b), incorporating both biotic resistance and abiotic resistance properties, prevents invasive plants from establishing and expanding their range, even if they have traits that enable them to overcome the climate factor. Trait values of the resident community, as an example of biotic resistance, will influence what may happen to an invasive plant. Niche theory, competitive exclusion, and limiting similarity all support the idea that invasive plants would not be able to establish in a resident community with native plants possessing the same trait values (Feng et al. 2019; Walder et al. 2019). According to prior adaptations theory (see previous section), populations evolve to be better adapted to certain environmental conditions based on their traits. This would also occur for invasives with trait also occur for invasives with trait values similar to the resident community, allowing for their increased establishment and (potential) expansion. While climate factors may allow invasive plants with the ability to tolerate abiotic conditions to become established and expand, ecosystem resistance

may either prevent invasive plants from being successful (Adler et al. 2013) or allow for coexistence.

Research on biotic resistance has more recently shifted to focus on resident community-level trait values. Community-weighted mean traits (CWM), calculated as the sum of the mean plant trait values multiplied by the mean biomass of each plant, and functional diversity (FD), a measure of the amount of dispersion in the trait values of plants in the resident community, have been used to estimate ecosystem processes, including biotic resistance (Diaz and Cabido 2001; Garnier et al. 2004; Mason and de Bello 2013). Resident communities with greater diversity appear to be more resistant to invasion (Fargione and Tilman 2005). In a study by Catford et al. (2019), CWM traits were a stronger measure of invasion risk than the trait values of an individual plant.

The ecosystem resistance factor includes all members of the resident community, including soil microbes, herbivores, pathogens, and top predators. Healthy, diverse, and fully functioning resident communities are less likely to become invaded. Disruptions to the resident community, such as disturbances due to habitat destruction, overgrazing, and agricultural activities, degrade ecosystem resistance factors and render these communities more vulnerable to invasion (Jauni et al. 2015). Invasive plants can disrupt food webs, reducing resident community resistance by altering nutrient cycling processes (Young et al. 2010). In addition, invasive plants may have the ability to produce molecules (e.g., allelopathic chemicals) that native soil microbes are not able to tolerate (the Novel Weapons Hypothesis), thus altering soil conditions and disrupting ecosystem resistance factors (Hierro and Callaway 2003). Invasive plants may promote the growth of soil pathogens that are especially harmful to native plants (Eppinga et al. 2006; Mangla and Inderjit 2008) or that attack the mycorrhizal fungi associated with them (Stinson et al. 2006). The symbiotic relationships with mycorrhizal fungi that are necessary for the growth of many native plants may not be required by invasive plants (Pringle

et al. 2009). These non-mycorrhizal invasive plants can alter the soil community by decreasing the abundance and availability of arbuscular mycorrhizal fungi (Aslani et al. 2019).

Invader Fitness The invader fitness factor (Fig. 2.3c) prevents invasive plants from establishing and expanding due to low fitness, even after overcoming the climate and ecosystem resistance factors. Invasive plants may have more phenotypic plasticity than naturalized or native plants, allowing them to achieve higher survival and reproductive success across a range of conditions, including “unfavorable” environments (Richards et al. 2006). One frequently discussed paradox in invasion science is the phenomenon of resident plant communities being invaded by individuals lacking the genetic variation representing the source populations (i.e., founder effects discussed in previous section), yet still able to quickly adapt and have high fitness in their new environment (Allendorf and Lundquist 2003; Schrieber and Lachmuth 2017). Multiple introductions from genetically distinct source populations can result in high genetic diversity within invasive population, genetic admixtures, and hybridization, which could explain increased invader fitness through the production of novel genotypes (Novak and Mack 1993; Novak and Mack 2001; Ellstrand and Schierenbeck 2006). Even without multiple introductions, founder effects do not appear to prevent invasive plants from becoming established in their introduced range, despite the reduction in genetic variation expected with such events (Dlugosch and Parker 2008). With sufficiently high adaptive genetic diversity, invasive plants are able to achieve high fitness and become established and expand (Dlugosch et al. 2015).

There are feedbacks and interactions among the factors of invader fitness, ecosystem resistance, and climate dynamics. For example, invasive plants may be better suited to adapt to ongoing climate change because they are already undergoing rapid phenotypic evolution enabling them to overcome the invader fitness factor (Nguyen et al. 2016). Evolution of earlier phenol-

ogy would lead to seed production prior to competition with natives when resources become limited, especially during drought conditions (Franks et al. 2007; Alexander and Levine 2019). An example of a possible interaction between the ecosystem resistance and the invader fitness factors is the adaptation to open habitats with high light levels, which can increase invader fitness in disturbed areas (Corliss and Sultan 2016). In this case, the “fast growth traits” of the invasive plants, as described earlier (e.g., high growth rates, high leaf nitrogen content), allow for them to overcome ecosystem resistance factors, which have the potential to lead to higher rates of nutrient cycling. Certain invasive plants, such as cheatgrass, can actually have an effect on the climate factor by changing abiotic conditions such as soil moisture content at the microsite scale, in a positive feedback mechanism (Ehrenfeld 2003).

2.2.3 Application of Spatial Scales

Spatial scale influences whether and how these three factors contribute to preventing invasion. For example, the ecosystem resistance factor, at local spatial scales, results in a negative relationship between plant richness and risk of invasion. Conversely, at regional scales, there may be a positive relationship between native and invasive plant richness due to climate factors or habitat heterogeneity (Kennedy et al. 2002; Davies et al. 2005). Spatial scales may also influence the degree to which invasive plants are phylogenetically related to natives. At local scales, invasive plants that are phylogenetically related to natives would be prevented from becoming established because they are more likely to occupy similar ecological niches. This suggests that a phylogenetic component may be somewhat associated with ecosystem resistance of communities. At regional scales, neutral processes and dispersal limitations could allow phylogenetically similar plants to establish (Thuiller et al. 2010). The effect of disturbance on invasion is also thought to be scale-dependent, with greater effects of disturbance on ecosystem resistance factors at local spatial scales and over longer temporal scales

(Jauni et al. 2015). Being mindful of the spatial scale of interest will help researchers to parse the relative contribution of the three factors in the IFF to an invasion. Essentially, our model can be used to assess the role of multiple processes, including interactive effects and feedbacks, across spatial scales, when assessing plant invasions.

2.3 Case Studies

The realization that invasive plants negatively impact native biodiversity and the environment, economies, and human health and well-being has resulted in research aimed at improving the understanding of the process and trying to lessen the impacts (Kumar and Singh 2020). Thus, an ever-growing body of research examining various aspects of invasion of resident plant communities, in particular, has been produced with useful insights. We conducted a systematic search of the literature and chose the most relevant and descriptive papers that used a “case study” format with a model plant being the focus. We examined the subcategories described by Young et al. (2017) for each factor (climate dynamics, ecosystem resistance, invader fitness) in the IFF model.

Case Studies: Climate Dynamics Historical climate conditions (based on 30-year averages), extreme high/low precipitation and temperature, duration of extremes, and rising atmospheric [CO₂] are the subcategories for climate dynamics that were described by Young et al. (2017) that would potentially allow for the establishment and expansion of invasive plants.

Adaptations to climate, and now extreme weather events, by invasive plants result in new community assemblages. Sheppard et al. (2016) report that Australian palm (*Archontophoenix cunninghamiana*), guava (*Psidium guajava*), and umbrella tree (*Schefflera actinophylla*) are introduced and now naturalized plants in New Zealand. The potential for these invasive plants to expand is predicted to increase with climate

change, and there is an increasing need to improve and/or incorporate best practice modeling, surveillance, and well-managed citizen science. In oak forests of northwest Spain, the evergreen shrub, silver wattle (*Acacia dealbata*), and blue gum tree (*Eucalyptus globulus*) have adapted to altered climatic conditions and expanded their range, as the native flora are slower to respond to the new weather patterns (González-Muñoz et al. 2014). The authors project that basal area increment (BAI) or the average area occupied by tree stems, will be positive (indicating an increase in tree size) for natives and negative (indicating an increase in number of trees) for silver wattle and bluegum. These findings are different from earlier studies, which did not account for climate change. In Hawai'i Volcanoes National Park, plants that have the C₄ photosynthetic pathway, including both invasive and native, are now found at higher elevations due to the climate change and an alteration of the fire regime (Angelo and Daehler 2013).

Invasive plants that have become established and are expanding under climate change often exhibit phenotypic plasticity, as described in the previous sections. In Chile, seed traits, specifically seed coat thickness and germination, of common dandelion (*Taraxacum officinale*) were evaluated in relation to climate variation (Molina-Montenegro et al. 2018). Thickness of seed coat decreased with latitude, while germination was highest in seeds originating from the southernmost part of the country. Bermudagrass (*Cynodon dactylon*), South African lovegrass (*Eragrostis plana*), Madagascar ragwort (*Senecio madagascariensis*), and common gorse (*Ulex europaeus*) are the most important invasive plants infesting grasslands of southern Brazil (Guido et al. 2016). The strongest correlation for all four invaders was with decreasing water due to climate change. Less correlated were road density (landscape structure) and land use (human activity). Packer et al. (2017) conducted a global assessment of the biology of common reed (*Phragmites australis*), which is particularly invasive in North and Central America, and projected declining populations in the British Isles and along the east coasts of the

United States and Panama. The latter due to rising sea levels associated with climate change.

Case Studies: Ecosystem Resistance The main features that comprise a plant community include species composition, macro- and micro-fauna, available nutrients, and soil type (Young et al. 2017). These have been examined in biological and physical contexts to assess ecosystem resistance to invasive plants (Levine et al. 2004).

Establishment of and resistance to non-native plants are two of the most common research topics in invasion plant biology. In a classic ecosystem resistance study, Houseman et al. (2014) assessed the invasion of sericea lespedeza (*Lespedeza cuneata*) in temperate grasslands of North America by creating models that included propagule pressure, soil fertility, and disturbance in relation to risk of invasion. Not surprisingly, they found that invasibility decreased as the soil fertility was enhanced and disturbance lessened. In an experimental grassland in Europe, increasing native plant richness reduced the above-ground growth of field scabious (*Knautia arvensis*), an invasive herbaceous perennial (Scherber et al. 2010). Compared to a species-poor community, the species rich one was more efficient in using resources and thus better able to resist invasion. Two more recently established invasive annuals, barbed goatgrass (*Aegilops triuncialis*) and medusahead (*Elymus caput-medusae*), in California grasslands, are effecting soil dynamics by reducing available nitrates in resident plant communities and lowering microbial biomass (Carey et al. 2017). Similar effects on soil N have been predicted to occur by increasing numbers of invasive symbiotic nitrogen-fixing lupines (*Lupinus* spp.) and birch (*Alnus* spp.) genera in the Boreal, subarctic, and upper montane temperate regions (Hiltbrunner et al. 2014).

In forest systems of the warm tropics to cold temperate regions, a large amount of research has documented many categories of ecosystem resistance. For example, eastern deciduous forests of New York and Connecticut, USA, were effective at resisting invasion by Norway maple (*Acer*

platanoides) if there was an intact and closed canopy. Dispersal and growth of maple stands were hampered by the lack of sunlight penetrating through the canopy. False brome (*Brachypodium sylvaticum*), an invasive grass in temperate forests of the Pacific Northwest, USA, was more common with soil disturbance and forest community structure: conifer forests being more invaded than deciduous forests (Taylor and Cruzan 2015). In tropical and subtropical forests of East Africa and China, respectively, an invasive tree (*Cinnamomum verum*) and two invasive herbs, mile-a-minute (*Mikania micrantha*) and eupatorium (*Eupatorium catariu*), were reported to effect soil microbes and fertility (Kueffer et al. 2007; Chen et al. 2017). The presence of soil mycorrhizal fungi was found to be more beneficial in resisting invasion of the two herbs in later succession forests, and nutrient poor soils were more conducive to invasion by *C. verum*.

Wetlands and riparian areas are very common systems in which ecosystem resistance to invasions has been tested, specifically the diversity of habitats and soil properties. In comparing invasive common reed (*Phragmites australis*) to native cordgrass (*Spartina* spp.), Allen et al. (2018) found no direct impact from soil biota, interspecific competition, or lack of nutrient availability on the invader. Renöfält et al. (2005) found no relationship between richness and invasiveness with the introduction of common sunflower (*Helianthus annuus*) in the Vindel River of Sweden; only substrate was important in limiting the invader. In wetlands of Zurich, Switzerland, invasive goldenrod (*Solidago gigantea*) affected the soil microbes and nutrients to the detriment of the resident plant community.

Case Studies: Invader Fitness The subcategories of plasticity, genetic mutation, phenological adaptation, and genetic selection compose the invader fitness factor in the IFF model (Young et al. 2017). These have been highlighted in the following case studies as plant hybridization, population genetics, and phenotypic plasticity.

Genome size, ploidy level, and mode of reproduction are topics that provide an assessment of

the role of genetic diversity in plant invasions (Burns et al. 2011; Te Beest et al. 2012; Suda et al. 2015). Giant goldenrod (*Solidago gigantea*) occurs as a diploid, tetraploid, and hexaploid in its native range of North America, while in its introduced range (Europe), only tetraploid populations are known (Schlaepfer et al. 2010). These cytotypes exhibit differences in the habitats they occupy and segregate geographically. In a global study, Nagy et al. (2018) assessed the performance of hexaploids in the introduced range of giant goldenrod and found that compared with tetraploids, they did not present a greater invasion risk. In Australia, two separate studies were conducted on plants from the Cucurbitaceae and Boraginaceae families to assess the role of invasive plant genetic diversity in establishment (Shaik et al. 2016). In the first study, paddy melon (*Cucumis myriocarpus*) and camel melon (*Citrullus lanatus*) were found to consist of a single genotype, suggesting one introduction event for each species. Desert gourd (*Citrullus colocynthis*), a related summer weed, was genetically diverse and thought to originate from multiple introductions. In the second study with two similar congeneric species (Shaik et al. 2016), Paterson's curse (*Echium plantagineum*) was found to be genetically diverse and highly invasive, whereas the other, common viper's bugloss (*Echium vulgare*), exhibited less genetic diversity and occupied a more limited ecological niche.

In addition to the level of genetic diversity within introduced populations, as described above, phenotypic plasticity can contribute to establishment success and increase the likelihood of invasion. For example, the invasion of smooth cordgrass (*Spartina alterniflora*) across much of China has apparently occurred due to plasticity of plant phenotypes that have matched local abiotic conditions, instead of adaptive evolution (Liu et al. 2016). Tufted knotweed (*Polygonum cespitosum*), a summer annual and recent invader in the Northeastern United States from Asia, has been found to exhibit high amounts of phenotypic plasticity, which would suggest an increased potential for invasiveness (Sultan and Matesanz 2015). The researchers detected higher fitness in all populations regardless of whether the habitat

was dominated by shade, sun, wet, or dry conditions. Similarly, Lamarque et al. (2013) found that boxelder maple (*Acer negundo*) genotypes did not increase trait plasticity but displayed genetic differentiation in southern and Eastern Europe, where it is highly invasive.

Hybridization, which is a form of genetic selection, is a routine occurrence among plants and has implications in terms of fitness of an invader and their establishment. In one study conducted in the salt marshes of San Francisco, California, invasive cordgrass (*S. alterniflora*) has been shown to hybridize with California cordgrass (*S. foliosa*), a native (Anttila et al. 1998). The invader produces greater amounts of pollen, which readily fertilizes the native. The resulting hybrids are more similar to the invader in trait characteristics and ability to adapt to changing conditions. In addition to habitat loss and decline in the native populations, the introgression through backcrossing has led to genetic pollution of the native.

While these case studies represent a large body of work, nonexistent are those that address all factors of the IFF simultaneously for any invasive plant (but see Young et al. 2017). Additional research, empirical and/or theoretical, is needed to comprehensively assess the effect of climate dynamics, ecosystem resistance, and invader fitness of invasive plants and those with the potential to become invasive. Such efforts will lead to a more comprehensive understanding of the invasion process and contribute to mitigating their negative effects through improved management.

2.4 Application of the IFF

We conclude this chapter with a discussion regarding how the three factors of the IFF model (climate dynamics, invader fitness, and ecosystem resistance), singly and synergistically, can be integrated into management decision-making. The IFF model provides a way to help determine what contributes to the establishment of non-native species and their range expansion during invasion. Such an assessment provides not only a better understanding of the invasion of native

plant communities but also a useful way to help improve management practices. The generalized invasion curve can be used to depict introduction, establishment, and expansion for invasive plants, but this curve can also be used to show how management approaches must adapt to changes in the population size and distribution of invasive plants (Fig. 2.1).

Pre-introduction The most ecologically and cost-effective management approach for curtailing plant invasions is preventing their introduction in the first place. This can only happen prior to the inflection point – the instant a propagule drops to the ground, attaches to a tree, or slips away into the water. Barriers, whether anthropogenic or natural, are the most sure way to curtail the invasion process. While border check stations and points of entry can halt human transport of invasive plant propagules, a lack of the ability to enforce laws to prohibit other routes (e.g., ocean vessels) and markets (e.g., internet) makes for a very porous system (Pyšek et al. 2020). The prevention of the introduction of invasive plants is ideal but in practice is nearly impossible to achieve.

Post-introduction Early detection rapid response (EDRR) is an approach for controlling non-native plants. The EDRR approach has been defined by the US Department of the Interior as “...a coordinated set of actions to find and eradicate potential invasive plants before they spread and cause harm...” (DOI 2016). Alternatively, Reaser et al. (2020) define EDRR as a “...a guiding principle for minimizing the impact of invasive plants in an expedited yet effective and cost efficient manner, where ‘detection’ is the process of observing and documenting an invasive plants, and ‘response’ is the process of reacting to the detection once the organism has been authoritatively identified and response options have been assessed.” The use of EDRR, while proposed by many (e.g., Maxwell et al. 2009; Pyšek and Richardson 2010; Littell et al. 2012; Antunes and Schamp 2017), has not been shown to be entirely effective. Largely, the lack of suc-

cess is knowing exactly how to implement “detection” and what the term “early” really means. Similarly, responses can vary and range from complete eradication of plants and propagules to partial or limited control of the target plant (Reaser et al. 2020). An EDRR approach has little need of understanding invasive plants beyond recognition and application of a removal technique.

Even before a non-native species has been introduced and EDRR applied, risk assessments of plant species can help determine potential negative impacts (e.g., costs) that occur during all phases of the generalized invasion curve (Meyers et al. 2020). Effectively assessing non-native plants for their risk is largely inadequate due to lack of data, transparency and repeatability, and uncertainty (Kumar and Singh 2020). However, risk assessments continue to be used by federal agencies when non-native species are initially detected, the status of a non-native species changes, and a potential pathway of introduction has been identified (Meyers et al. 2020). In California, USA, and likely other arid regions, the public is encouraged to use drought-tolerant plants in order to reduce water use. The result is an abundance of plants with drought-tolerant characteristics, which over time have an increasing likelihood of becoming invasive (Pemberton and Liu 2009).

Establishment and Range Expansion During the establishment phase of an invasion, as population size and/or population number increases, eradication may still be possible. But, as populations increase in size and expand their distribution, other approaches, such as containment and “asset-based protection,” are required (the latter focuses on the protection of farmlands, industries, recreational areas, and natural ecosystems). Each of the three factor of the IFF must be overcome for a non-native species to expand its range. Thus, it is critically important to better understanding of how these factors can influence non-native establishment and range expansion (e.g., invasion process) to predict which plant communities are likely to be invaded in the future. This

means that management strategies should rapidly shift from eradication, to containment, to asset-based protection, as the pace of an invasion quickens.

Employing the IFF Any one of the three factors of the IFF model can terminate the potential that an invasion will occur, so all of them should be taken into account by researchers or managers. Using the IFF model, a qualitative and quantitative snapshot about a potential or current plant invasion can be generated based on published research (Young et al. 2017). The IFF model should be considered a tool to establish research priorities and identify components in the invasion process that can be used to facilitate eradication, containment, or asset-based protection. Several recent papers have identified a “knowledge gap” or disconnect between research and practice in the management of invasive plants (Funk et al. 2020; Pyšek et al. 2020; Young and Kettenring 2020).

Additionally, the IFF model can be used to inform the removal of invasive species and the restoration of native communities. In the restoration of a site dominated by invasive plants, the first step (i.e., site preparation phase) frequently involves the physical and/or chemical removal of the invaders (Rowe 2010). Immediately afterwards, native plants are seeded or planted to fill vacant niches and prevent subsequent reinvasion by the same or other invasive plants (Masters and Sheley 2001; Hulme 2006). The overall goal of these efforts is to assemble an invasion-resistant community, so practitioners involved in ecological restoration should establish native plant species with a diversity of phenotypic traits, including those that have unique phenology, growth rate, and stress-tolerant abilities (Kimball et al. 2016). For problematic invasive plants, which have, by definition, overcome all three factors of the IFF model, restoration efforts should include plant species that have specific ecological niches to establish native communities with different ecosystem resistance characteristics, compared to the community that was initially invaded.

In this manner, it may be possible to reestablish the ecosystem resistance factor (dotted line in Fig. 2.1).

When speed of invasion, pathways of distribution, and evolutionary changes of invasive plants are not well known, information from an IFF model can be used to improve the effectiveness of management programs and tools. Funk et al. (2020) listed soil seedbank dynamics, life history traits, and the effects of ongoing climate change as important plant invasion ecology knowledge gaps identified by land managers that researchers should fill. The three factors of the IFF model address each of these gaps: ecosystem resistance (additions to and loss of seeds in soil seedbanks), invader fitness (adaptations linked to life history trait evolution), and climate dynamics (the range of climates, including extreme weather events, that an invasive species can tolerate). Young et al. (2017) used musk thistle (*Carduus nutans*) as an example of how the IFF could be applied to help focus research to answer basic questions and address management challenges. Musk thistle, a problematic invasive plant around the globe (Shea and Kelly 2004), “failed” to become established in a native perennial grassland of the Central United States (Young 2015). Using the IFF model, empirical studies conducted on musk thistle (see Young et al. 2017) provided evidence to suggest that musk thistle did not exhibit phenotypic plasticity (invader fitness) in these perennial grasslands during extreme drought (climate dynamics), leading to the inability of the plant to become established in this region.

2.5 Conclusions

By conducting research using the IFF model, a better understanding of how climate dynamics, ecosystem resistance, and invader fitness influence the eventual fate of non-native plants can be obtained. This knowledge can be used to improve decision-making by land managers to help mitigate the negative consequences of invasive plants, especially the invasion of native plant communities.

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Development of Pathways of Global Plant Invasions in Space and Time

3

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Abstract

Humans have exchanged plant species beyond their native borders since millennia. The pathways of exchange and their relative importance have differed among regions, times and species. Here, we review the temporal developments of pathways of alien plant species introductions and how these relate to trends in alien plant species richness at a global scale. Although the rate of exchange of alien plants has grown steadily over time, significant advancements in human technological progress initiated new bursts of acceleration in

global spread. Examples include the discovery of new seaways around 1500, the start of modern industrialisation in the early nineteenth century and the rise of global trade and human prosperity after World War II. Apart from a continuous intensification, the relative importance of pathways remained surprisingly stable. During the last 500 years, the introduction of plant species for cultivation represents the dominating pathway and was associated with more than half of all introductions. Although the relationship between horticulture and the occurrence of alien plants is often difficult to prove, the huge number of plants cultivated in the world makes it likely that, in the future, many introductions will continue to originate from private or public gardens. Indeed, horticulture remains the only introduction pathway which, up to now, has increased in relative importance among all pathways globally. Despite the rising awareness of the issues of introducing new alien species, the current socio-economic developments indicate that we have to expect many more alien plant species to come in the future.

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Biological invasions · Globalisation · Historic · Long term · Neophytes · Time series · Weeds

3.1 Introduction

Humans have been very successful at redistributing plant species worldwide by introducing them to regions outside their native range. We currently know of >13,000 naturalised alien plant species worldwide (Pyšek et al. 2017). These alien plant species are unevenly distributed across the globe with major hot spots located in Europe, North America and Australasia (van Kleunen et al. 2015). This should come as no surprise, because in contrast to native plant species, the distribution of alien plant species is primarily a result of human activity. In fact, a major determinant of the global distribution of naturalised alien plant species is the frequency and intensity of their introduction (Essl et al. 2010), which is determined by the way they entered a new region.

Alien plant species have been introduced in a number of different ways and for various reasons, but in most cases introductions were related to food production, ornamental purposes and accidental releases (Saul et al. 2017; Pergl et al. 2020). These causes of introduction – the so-called pathways of biological invasions – can vary distinctly among species, regions and over time (Essl et al. 2015). Even for the same species, the pathway may vary in space and time, and many species have been introduced through multiple pathways.

Changes in global alien species richness are tightly coupled to changes in international pathway dynamics, and the former is difficult to understand without having a basic knowledge about variation in the latter. The number of alien plant species increased sharply during recent centuries worldwide (Seebens et al. 2017). Europe experienced a pronounced increase from 1500 onwards (Fig. 3.1), while alien plant species numbers in Asia, the Pacific and the Americas caught up during the nineteenth century and finally reached a similar level compared to Europe today. Not only did the number of alien plant species increase, but also the rate of increase became more rapid, which indicates a worldwide acceleration of establishment events and most

likely introductions of alien plant species since the early 1800s (Fig. 3.1). There are indications that the acceleration slowed down, particularly in North America, during recent decades (Seebens et al. 2017), but the level still remains very high with an annual mean rate of 50 new alien plant species that have never been recorded before becoming established worldwide, as a result of a continuous increase in the accessibility of source pools of new alien plant species (Seebens et al. 2018).

According to the Convention on Biological Diversity (CBD 2014), pathways of introduction denote mechanisms through which “alien species may arrive and enter a new region”. The categorisation adopted by the CBD is based on the framework proposed by Hulme et al. (2008) and contains six major pathways (release, escape, contaminant, stowaway, corridor and unaided) and several subcategories (Fig. 3.2). The first three are related to the transport of a commodity, which may be either the species itself (release, escape) or something else such as soil within which seeds are accidentally included (contaminant). Another criterion for the categorisation of these pathways is whether the alien plant species was introduced intentionally (release) or unintentionally (contaminant). Pathways may also include combinations of both such as the intentional planting in a garden and the subsequent unintentional spread beyond the garden fence (escape). The fourth pathway (stowaway) relates to species attached to a vector, which is moving itself such as a car or a ship or transported on gardening equipment or clothes, etc. The introduction via this pathway is also unintentional. The last two pathways (corridor, unaided) describe the secondary spread of species from neighbouring regions without the direct intervention of human agency. In the first case (corridor), this may happen along a newly constructed corridor, such as a new road. In the second case (unaided), secondary spread is not restricted to corridors but can occur through natural dispersal via wind, water or animals.

3.2 Historical Developments of Introduction Pathways and Establishments of Alien Plants

Given the long history of human-mediated plant introductions and the intense temporal changes in socio-economic activities, it seems likely that the pathways of alien plant species introduction have changed over time (Essl et al. 2015). To understand the distribution of alien plant species observed today, it is therefore essential to get a thorough understanding of the dynamics of pathways and establishment of alien plant species over recent centuries. We provide an overview of

the historical developments of both pathways and biological invasions of plants below.

3.2.1 Early Spread of Alien Plants

Information about the spread of plant species in early times (before 1500 AD) is very scarce and associated with a high degree of uncertainty (Crees and Turvey 2015; Essl et al. 2018). The unintentional spread of plants by humans very likely has been ongoing for thousands of years, but in many cases, information on specific introduction events is lacking. Humans have moved plants across large distances both deliberately for

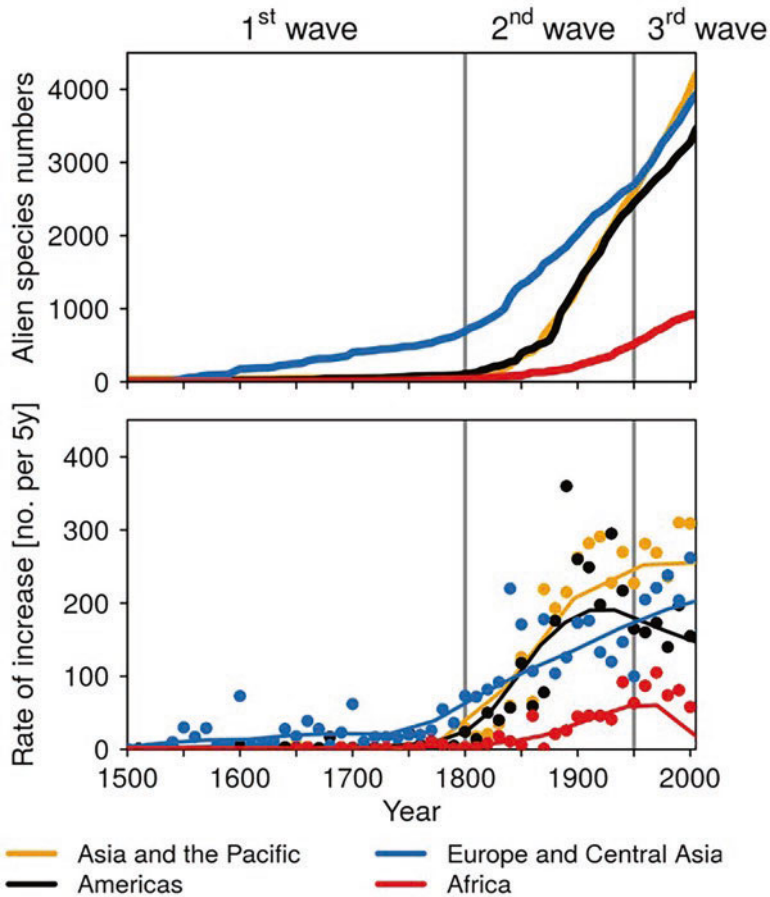


Fig. 3.1 Time series of established alien plant species numbers (upper panel) and the rates of increase (lower panel) for different continental regions. The three distinct

waves (periods) of plant species naturalisation discussed in the main text are indicated by vertical lines. Data source: First Record Database (Seebens et al. 2017)

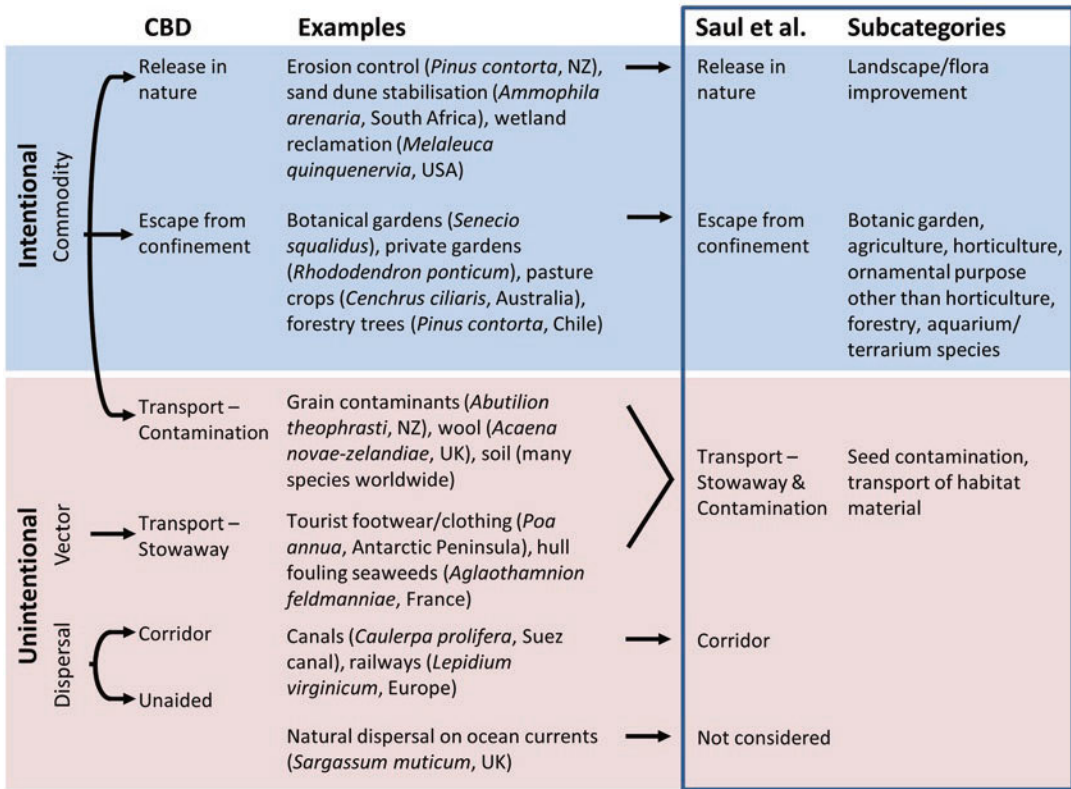


Fig. 3.2 Major pathways of biological invasions following the classification by the Convention on Biological Diversity (CBD 2014) with examples. Pathways were adapted and grouped based on data availability in a recent

study (Saul et al. 2017), which provides the data source for the analysis presented in this chapter. We selected data for the most important subcategories, which represent 96% of all reported invasion events

food and ornament (Reichard and White 2001; van Kleunen et al. 2018a) and by accident such as on their clothing or on the fur of domesticated livestock. In contrast, the intentional introduction of alien plant species has been reported occasionally. Evidence indicates that as early as the Late Pleistocene onwards, modern humans transported plant species as food crops, medicinal plants or for ornamental purposes (Boivin et al. 2016; van Kleunen et al. 2018a). In more recent times, examples from around the world revealed that plant species have been exchanged over larger distances. For example, agricultural crops were imported by the Pharaohs of ancient Egypt as early as 3000 to 1500 years ago (Janick 2007), and at around the same time, plants were traded in Panama and other parts of Central America (Sánchez 1997). The Greek physician Hippocrates reported medicinal plants imported from India in

the fifth century BC (Fry 2017). From 200 BC onwards, one of the first intercontinental trade routes, the Silk Route, was established, which connected East Asia with Central Asia, Europe and parts of Africa. This route was used to exchange various kinds of plant species (Spengler et al. 2018). In Europe, the expansion of agriculture from Mesopotamia to Central Europe, and subsequently to Western and Northern Europe, resulted in the intentional introduction of the first set of agriculturally used plant species and in the unintentional spread of species which were adapted to the new selection pressures introduced by farming communities from several thousand years ago (Crees and Turvey 2015). Later, the Greeks and the Romans transported plant species throughout the Mediterranean region and also introduced species to regions outside their native ranges (di Castri 1989). For example, the spread

of the edible European chestnut (*Castanea sativa*) has been attributed to the expansion of the Roman Empire (Conedera et al. 2004). Around the same time, supplies of cloves, nutmeg, mace and sandalwood from Indonesia were reaching China, India, western Asia and the Mediterranean (Donkin 2003). On the other side of the globe, from around 200 BC to 1,000 AD, the Polynesians developed impressive navigational skills. This allowed them to reach Pacific Islands spanning from New Zealand to Hawaii, where they introduced various crop and fibre species (Cox and Banack 1991). First gardens with plant species from very distant regions have been reported from Mexico, such as those from the Aztec king Moctezuma I (Sanchéz 1997). In medieval Europe, alien plant species, usually from the Mediterranean, were planted near castles, and this is still reflected in the floras around Central European castles (Dehnen-Schmutz 2004).

Before the fifteenth century AD, long-distance transport of plants by humans between continents occurred only rarely. Journeys were burdensome and dangerous, and only a few explorers and adventurers, such as Marco Polo in the thirteenth century, dared to travel long distances, bringing back materials and stories of unusual plants. Most of the introduced species were planted for medical purposes or as food crops. This pathway of introduction can be considered as being unintentional escape. Only in a few cases, like the planting of trees by the Romans allegedly to feed their troops (Kannan et al. 2013) or the introduction of bottle gourd (*Lagenaria siceraria*) by Polynesians in the Pacific region (Clarke et al. 2006), introductions may qualify as intentional releases.

In the late fifteenth century, Europeans started to explore the outer margins of their known world in a strategic and organised way, which resulted in the discovery of new seaways between Europe, Africa, East Asia and the Americas. This represents the onset of the development of an intercontinental trade network, which has continued to grow and intensify until today. Because of the huge impact this globalisation of trade and transport had on the spread of alien species, ecologists, particularly in Europe (Richardson et al. 2000), use 1500 as a temporal threshold to distin-

guish between archaeophytes (<1500) and neophytes (>1500). Although the exchange of plant species has intensified continuously until today, we can distinguish phases of intensification, which we call “waves of global spread”. We distinguish the timing of the waves based on marked changes in socio-economic activity and pathway dynamics and associated increases in numbers of alien plant species (di Castri 1989; Seebens et al. 2017). The temporal dynamics of socio-economic activities certainly varied across continents in timing and intensity, and so were the dynamics of alien plant invasions (Seebens et al. 2017). The timings of the waves, as described below, may therefore differ depending on the region; however, our distinction of waves should be considered as a general categorisation applicable in modified ways to a variety of circumstances worldwide and presented here based predominantly on examples with mostly global implications.

3.2.2 The 1st Wave of Global Spread (1500–1800): The Age of Exploration

The period from the beginning of the sixteenth century to the end of the eighteenth century, often termed the Age of Exploration, was characterised by extensive overseas exploration and the widespread adoption in Europe of colonialism and mercantilism. Contact between the Old World (Europe, Asia and Africa) and the New World (the Americas and Australia) resulted in the transfer of many plants, a large number of which became established in the wild in these new ranges. Many Old World crops such as carrots (*Daucus carota*), hops (*Humulus lupulus*) and turnips (*Brassica rapa*) became naturalised in the New World soon after colonisation by Europeans (Aikio et al. 2010). In contrast, several plant species brought from the New World as ornamentals or food plants became established in the Old World like prickly pear (*Opuntia* spp.) and Indian shot (*Canna indica*).

Major aims of the first journeys were to explore further possibilities for trade and exploi-

tation of new resources. Back in Europe, the explorers praised their new findings and reported on them in often exaggerated ways (Sarnowsky 2016). This raised curiosity in unusual or striking life forms, and the scientific aspects of explorations grew in importance. For example, in 1492 Christopher Columbus wrote in his log book that the many plants that he found on the island of Isabella could be of economic interest for the production of dyes, medicine and spices and that he wanted to take samples of most of these plants home with him (Stöcklin et al. 2003). Naturalists joined the journeys of the explorers and tradesmen to inspect and report on the foreign flora and fauna. In the 1570s, Francisco Hernández was sent by the Spanish king to Mexico and other regions of the New World to collect plants and to get a better understanding of their local use, which is considered to be the first expedition of nature undertaken by a government (Fry 2017).

In the following centuries, Europeans continuously intensified and expanded their trade network. An important role in the maintenance and expansion of the infrastructure was played by the British East India Company founded in 1600. Together with competitors, like the Dutch East India Company, they established a global, mostly seaborne, trade network connecting Europe with the Americas, Africa and South and Southeast Asia. With the expansion of the European trade network, the worldwide exchange of plant species grew likewise in all directions (“Columbian exchange”, Crosby 1972). The foundation of new settlements to support the trading activities led to the introduction of mostly European crop plants into regions all around the world. In addition, plants have been introduced unintentionally as stowaways or contaminants, though information about these introductions is limited (Mack and Erneberg 2002). The rising numbers of emigrants from Europe to the newly colonised regions generated a demand for a more systematic investigation of suitable crop plants for the different regions, which was performed by the early botanic gardens and the later founded Acclimatisation Societies. The latter aimed at “improving” nature for colonial settlers by intro-

ducing species familiar to and useful for settlers (Dunlap 1997). As a consequence, Europe is considered to be a net exporter of alien plant species during that time, which is described as the “Imperialist Dogma” (Drake et al. 1989) or “Ecological Imperialism” (Crosby 2015). Indeed, Europe has donated 288% more naturalised plant species to the rest of the world than one would expect based on the size of the native European flora (van Kleunen et al. 2015).

The number of alien plant species in Europe continuously grew (Fig. 3.1). Bringing back an increasing number of alien plant species initiated the establishment of botanic gardens throughout Europe, as well as in its overseas colonies. Here species were planted not only for medicinal purposes but also for aesthetics. In 1545, the first botanic garden in Europe was opened in Padua, Italy, where plant species were grown specifically for research and education, originating from the regions of the Balkan, Levant and Americas (Fry 2017). Other botanic gardens followed later, such as the Jardin du Roi in Paris, France, (1626), Company’s Garden in Cape Town, South Africa, (1652), Chelsea Physic Garden in London, United Kingdom (1673), and the El Real Jardín Botánico del Soto de Migas Calientes in Madrid, Spain (1755). In 1759, one of the largest and most influential botanic gardens worldwide, the Royal Botanic Gardens at Kew in London, was founded with the ambitious aim to showcase all known plants on Earth (Fry 2017). Already in these times, the gardens contained a huge number of plant species from all over the world. The Jardin du Roi in Paris alone, for example, displayed 6,000 plant species in 1788 (Fry 2017), and the Royal Botanic Gardens at Kew had >9,000 plant species in 1814 (Aiton 1814). The purpose of these gardens was not only to present a wide diversity of plant collections but also to support gardens in other parts of the world, to educate scientists and perform experiments in order to identify species of potential interest for transplanting to new regions. In the course of time, the larger botanic gardens developed global networks for exchanging plants and plant materials, particularly among the colonial territories of the

respective empires. For example, King Carlos III of Spain decreed the establishment of a botanic garden on Tenerife for the acclimatisation of alien plants from the Spanish territories in South and Central America, before they would be planted in Madrid (<https://www.tenerife-information-centre.com/botanical-gardens-puerto.html>). Thus, botanic gardens played a major role for introducing new species and acted as entry points for both intentional and unintentional introductions of alien plant species (Hulme 2011).

Within the first wave of global spread from 1500 to 1800, the vast majority of established alien plants – at least from those, we are aware of – had been introduced as ornamental or crop plants. This is reflected in the temporal development of the importance of pathways (Fig. 3.3). Although such an analysis underlies the strong assumption that pathways did not change for the same species over time and space, it provides a reasonable estimate of the temporal development of pathways. By 1800, 21% of all plant species considered in this analysis had been introduced somewhere in the world. The five most widespread introduced plant species during this time period were common guava (*Psidium guajava*) (22 countries), horseweed (*Erigeron canadensis*) (13 countries), jimsonweed (*Datura stramonium*) (8 countries), calamus (*Acorus calamus*) (8 countries) and southernwood (*Artemisia abrotanum*) (4 countries), which have been introduced by escape from confinement (63%), by release in nature (23%) and by transport (14%). Across all plants, the dominant pathway for plant introduction until 1800 was escape from confinement (58%), such as from botanic gardens, parks and agriculture. The intentional release in nature only played a minor role (17%). Likewise, unintentional introduction through contaminant or stow-away contributed less to the overall number of plant introductions (25%), but this may be biased by a lack of reports. However, compared to the period after 1800, the intensity of spread was relatively low during the first wave of global spread of alien plant species.

3.2.3 The 2nd Wave of Global Spread (1800–1950): The Age of Industrialisation

In the nineteenth century, the number of alien plant species distinctly rose at a continuously accelerating rate until the end of the century (Fig. 3.1). The reasons for this increase are manifold but mostly rooted in the acceleration of globalisation of trade and transport and the increased welfare of societies. Technological innovations such as the shift from wooden vessels powered by wind to iron-hulled vessels powered by steam not only permitted faster crossings of oceans and transport of larger numbers of people and volumes of commodities but also led to new trade routes opening up that were less dependent on wind (Gardiner and Greenhill 1993). Between around 1800 and 1900, most colonial empires were at their peak, and large parts of the world were divided among a few colonial powers (Lenzner et al. 2018). Trading activities were particularly intense among regions belonging to the same colonial powers. Members of these empires benefitted economically and experienced increases in trade between 1870 and 1913 that were up to 270% higher compared to regions outside these empires (Mitchener and Weidenmier 2008). As a consequence of the industrial revolution, trade volumes and prosperity of the European countries accelerated distinctly (O'Rourke et al. 2008). Besides the pure rise in trade volumes, the global trade network became increasingly interconnected, and new goods that were not or rarely traded before were traded frequently. New links in the trade network also connected more species pools and allowed more species to be intentionally or unintentionally introduced to new regions. This resulted in an increased accessibility of source pools of alien plant species, which distinctly increased at around 1850 (Seebens et al. 2018).

In addition to trade, human migration started to play an increasing role in the spread of plant species. Emigration out of Europe particularly towards North America, Australia and New

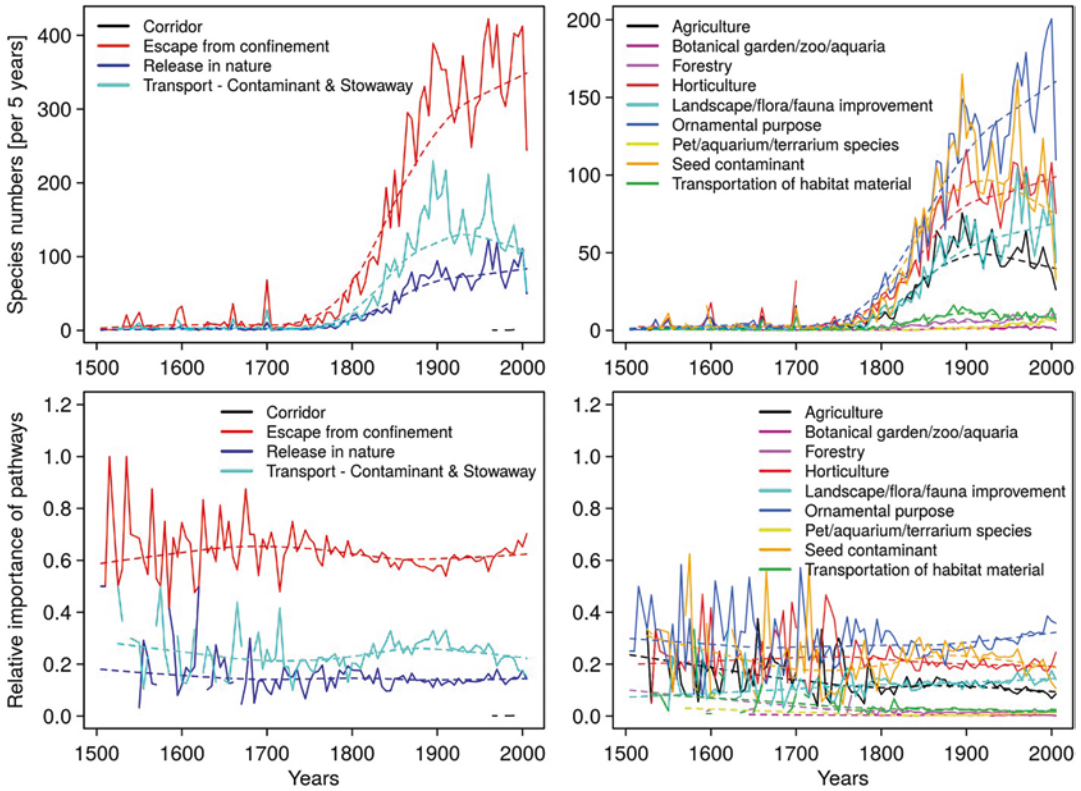


Fig. 3.3 Time series of the absolute and relative importance of main categories of pathways for the introduction of alien plants (left panels) and of a selection of important subcategories (right panels). Pathway information was obtained from Saul et al. (2017) and is based on the databases “Delivering Alien Invasive Species in Europe” (DAISIE; <http://www.europe-aliens.org/>) and “Global Invasive Species Database” (GISD; <http://www.iucngisd.org/gisd/>).

Combined with the First Record Database, which provides the year of first record of an alien species in a country (Seebens et al. 2017), the database used here included altogether 30,828 combinations of species, pathway, country and year for a total of 2,198 plant species. Species associated with multiple pathways were counted proportionally so that each combination contributed a total of one to the pathway analysis

Zealand increased tremendously in the nineteenth century. This migration wave was triggered by rising human population sizes and severe famines in Europe. Stories about fertile soils, wealth and free and pleasant living conditions in the colonies attracted many people. In addition, many convicts were sent to the colonies to occupy the new lands (Butler 1896). Altogether, this resulted in mass migration waves towards North America, parts of South America and Australasia. The European settlers brought a large number of species to these new regions (di Castri 1989; Crosby 2015). This caused a dramatic increase in alien plant species numbers in Australasia and a peak in alien plant introductions in North America

with ca. 30 newly established plant species recorded annually in the late nineteenth century (Seebens et al. 2017). The introduction of new species was supported by the networks of acclimatisation societies and botanic gardens. By 1900, there were reportedly around 50 acclimatisation societies, which intentionally introduced foreign species, and the British botanic garden network consisted of over 100 botanic gardens worldwide, which frequently exchanged species (Osborne 2000).

Accompanied with the increase in prosperity, horticulture was not restricted anymore to the gardens of wealthy people and public greens. While botanic gardens still remain a source for

the escape of alien plants into the wild until today (Hulme 2011; van Kleunen et al. 2018a), the interest in growing alien plants in domestic gardens rose among Europeans, thereby considerably increasing colonisation and propagule pressure of alien species. This was the time of the so-called plant hunters (Tyler-Whittle 1997): botanists and adventurers who travelled around the world to collect unusual or rare plants attractive for botanic gardens and the horticultural industry (e.g. nurseries), particularly in Europe and North America (Stoner and Hummer 2007). Plant hunters brought thousands of plant species to Europe, and many of these plants were subsequently introduced by Europeans to their colonial empires (e.g. Kannan et al. 2013); many of them became additions to the wild local floras. The successful transportation of living plants over longer distances was boosted by technical advances and inventions. The Wardian Case, for instance, was a small portable greenhouse, which allowed the plant to grow under stable conditions during transport (Fry 2017), and the development of steamships enabled faster, more distant and more frequent travels (Gardiner and Greenhill 1993). This enhanced the chances of plant survival significantly and revolutionised the trade and transport of living plants (Tyler-Whittle 1997).

The intensification of trade, migration and horticultural activities were the main drivers of the introduction of alien plant species during the 2nd wave of the global spread. By 1950, 85% of all alien plants recorded in our analysis had been introduced at least once somewhere in the world. Thus, the second wave of global spread represents the time period with the most intense introduction of alien plant species across all time periods. The five most frequently introduced species during 1800 to 1950 were *Datura stramonium* (31 countries), *Medicago sativa* (29 countries), *Lepidium virginicum* (28 countries), *Galinsoga parviflora* (27 countries) and *Elodea canadensis* (27 countries). All of these five species have been introduced via escape from confinement, intentional release and transport according to Saul et al. (2017). Across all plant species introduced until 1950, most species have been introduced intentionally, which is reflected

in the distinct increase in the importance of the escape from confinement pathway such as horticulture, agriculture and forestry (Fig. 3.3). Other deliberately planted species have been released to improve the “impoverished” local flora and landscape (Robinson 1870). The second largest pathway at that time, transport as seed contaminants, indicates the intensification of trade and transport including human migration. For example, the ballast soil used to stabilise the ships was frequently contaminated with seeds of European weeds (Brown 1879). The movement of vehicles and people thus provided a range of opportunities for plants to stowaway across the world, and, with the increase in global transport, the importance of seed contamination rose likewise. In relative terms, 53% of all alien plants have been introduced until 1950 as escapes from confinement, while 29% introductions could be related to transport, 17% to intentional releases and less than 1% via a new corridor (Fig. 3.2). As none of these pathways were managed in any form, the spread of alien plant species continued to accelerate during the nineteenth century (Fig. 3.1).

Another important historical change not captured so far is the change of land use from pristine environments to pastures, croplands and urban areas. Although land use change does not represent an introduction pathway according to the CBD (CBD 2014), it is an important driver of the spread of alien plants (Pauchard and Alaback 2004; Seebens et al. 2018). This is also reflected in the observation that most naturalised species come from anthropogenic habitats (Kalusová et al. 2017) and naturalised there (Clements et al. 2004). The steep rise in global human population size created a huge demand for areas of food production and living. Land use intensified distinctly in the nineteenth century worldwide across all major biomes suitable for human life (Ellis et al. 2010). By 1900, around 30% of the ice-free land was transformed to used land – the so-called anthromes (Ellis et al. 2010). The creation of disturbed and novel habitats made resident communities more susceptible to invasions and provided opportunities for establishment of alien species (Catford et al. 2012). The intensification of land use went hand in hand with the intensification of

introductions, which together resulted in the strong increases in established alien plant species worldwide (Fig. 3.1). For example, the weed floras in arable crops of the New World largely reflect the European and Mediterranean source pool (Ikegami et al. 2019).

After World War I and until the end of World War II, the dominance of the European colonial empires declined. Several colonies gained independence, and the once very influential East India companies lost influence and power as the national governments took over the privileges and rights of the companies. However, the trade routes, markets and horticultural supply chains remained and laid the foundation for the third wave of global spread of alien species.

3.2.4 The 3rd Wave of Global Spread (1950–Present): The Age of Globalisation

The foundation for the 3rd wave of global spread, from 1950 until today, was laid already in the nineteenth century. Many of the trends characterising the development of society and economy during 1800–1950 accelerated even faster after World War II. The dominance of the European economies continued to decline, mostly because other countries caught up reaching similar levels of economic prosperity. Europe turned from a net exporter of plant species to a net importer (Drake et al. 1989; Seebens et al. 2015). Technical advances in engineering and the still ongoing industrialisation of labour together with an increasing number of free trade agreements boosted international trade once more. Containerised transport started its story of success in the 1950s. It revolutionised global transport once more, as it enabled an efficient way of exchanging commodities, but also resulted in an increasing movement of alien species. Air transport became more important, and international tourism began to flourish worldwide, thereby accessing even remote islands and continental regions. The expansion of transport infrastructures facilitated the further spread into formerly less connected regions with the potential to intro-

duce alien species also to remote places (Seebens 2019). Human population size increased even stronger than before 1950, and this further enhanced the demand for land needed for food production and human living. By 2000, 55% of the total ice-free land was covered by anthropogenically transformed habitats (Ellis et al. 2010).

Likewise, the number of alien plant species has been growing continuously until today, although at lower pace than during the second wave of global spread (Fig. 3.1). In absolute terms, the number of introduction events associated with these pathways stabilised at high levels or even showed first indications of decline (Fig. 3.3). From 1950 until today, the five most frequently introduced species based on the data set obtained from Saul et al. (2017) were water hyacinth (*Eichhornia crassipes*) (15 countries), pitchfork weed (*Bidens frondosa*) (14 countries), waterweed (*Egeria densa*) (12 countries), devil weed (*Chromolaena odorata*) (11 countries) and red amaranth (*Amaranthus cruentus*) (10 countries). All of them are known to be introduced along the three dominating pathways, escape from confinement, intentional release and transport. Among all plants in the database used here, 56% escaped from confinement in the time period from 1950 until today, 24% have been accidentally released through transport, while 19% were intentionally released and less than 1% immigrated through new corridors. This list of most frequently introduced alien plant species and their distribution differs compared to what has been reported elsewhere (Pyšek et al. 2017) since the data set used here (1) represents only a subset of all known alien plant species (2,198 species considered here compared to 13,168 from Pyšek et al. 2017), as it includes only species with associated pathway information; (2) is restricted to a coarser spatial resolution as pathway information is only available on national scales, while others provided information on sub-national units (van Kleunen et al. 2015); and (3) has a strong bias towards Europe because of the underlying pathway databases (Saul et al. 2017).

Over all three waves, the relative proportion of main pathways remained rather stable. Not surprisingly, the relative importance of the full time

period from 1500 until today is similar to those reported for the individual waves: 54% escape from confinement, 28% transport, 18% intentional release and <1% corridor. Time series of subcategories of pathways revealed that only the pathways ornamental purpose and horticulture showed a clear ever-increasing trend over all waves, while others such as agriculture or seed contamination indicated stabilisation or slight declines in the most recent decades (Fig. 3.2). However, clear trends are difficult to reveal giving the high variation and uncertainty in the data.

The aforementioned changes in pathways and alien plant species numbers are considered to represent general dynamics at a global scale, while at smaller scales temporal developments may deviate from the described patterns. In fact, intercontinental variation of the phases of invasion waves is already apparent in Fig. 3.1, and other studies reported different timings at smaller geographic scales. For instance, a wave of expansion of alien species has been reported in Chile during 1910–1940, which coincides with a strong growth in Chilean agriculture (Fuentes et al. 2008). This relates to what is here described as the 2nd wave of invasion, characterised by industrial developments and agricultural intensification but shifted in time. As another example, South Africa revealed similar wave-like dynamics but with different timings such as the arrival of European settlers in 1652, according to the onset of the 1st wave, and an increasing growth of the agricultural sector after 1850 similar to the 2nd wave (Canavan et al. 2019). In New Zealand the shift from species largely introduced unintentionally to those arising from deliberate horticultural imports occurred in the 1950s (Hulme 2020). Furthermore, dynamics of pathways and alien species numbers can clearly deviate if the sites were decoupled from the general dynamics of globalisation such as remote islands, where invasion dynamics are often affected by individual events such as first settlements and the establishment of research stations (Frenot et al. 2001). In other cases, individual empires such as those by the Romans in the Mediterranean area or the Polynesians in the Pacific area had distinct influences on the spread of alien plant species within

their range (Conedera et al. 2004; Kirch 2017), which might be considered as a wave on its own for the specific regions. Common to all regions, however, is that the trajectories of introduction and expansion of alien plant species show clear waves of accelerations although at different time points. Thus, the concept of invasion waves seems to be valuable to a wide range of sites at different scales.

3.3 Visualising the Future of Plant Invasion Pathways

The number of alien plant species increased continuously, and the rate of increase remained at a high level during the last decades (Seebens et al. 2017). In addition, source pools of alien plant species have been extended due to the increased interconnectivity of regions worldwide. This resulted in an increase in the number of new alien plant species, which had never been recorded before as being alien elsewhere in the world (Seebens et al. 2018). Hence, based on observed trends during the last decades, we have to expect more alien plant species to come in the future (Bradley et al. 2012; Seebens et al. 2021). Indeed, predictions based on lag times between introduction and detection revealed clear increases in species numbers particularly in emerging economies (Seebens et al. 2015). Lag times due to delays in detection and reporting play an important role in biological invasions and cause changes in pathways and management dynamics to be apparent in species numbers only after decades (Crooks 2005; van Kleunen et al. 2018b). The increasing trends in alien plants species numbers is supported from a pathway perspective as the dominant pathways of introductions such as ornamental purpose or horticulture show clear upward trends (Fig. 3.3). Only introductions via the transport, contamination and stowaway pathways seemed to have declined in absolute and relative importance recently.

Although most of the dynamics observed in the past indicate a continuation of increases in alien plants species numbers, evaluations of future dynamics are challenging for various rea-

sons. Interacting effects of different drivers of global change such as climate change or land use changes can have complex effects on the distribution of alien plants and might also result in range contractions (Bradley et al. 2010), which are difficult to evaluate at a global scale. In addition, future trajectories of two other factors, namely, horticulture and management, crucial for the introduction and establishment of alien plant species are difficult to assess. Horticulture in its broader sense has been a major pathway for alien plant species (Fig. 3.3), but how horticulture will develop in the future and how this will affect the introduction and establishment is difficult to predict (Drew et al. 2010). As another factor, strategies and policies to mitigate biological invasions have been put in place in various countries, and more can be expected to come (Hulme et al. 2018). A proper management of pathways and alien species can have distinct influences on the development of alien species trajectories (Simberloff et al. 2013). We will address both factors in more detail below.

3.3.1 The Prominent Role of Horticulture in the Spread of Alien Plants

There is strong evidence that horticulture is a major pathway for plant invasions in many parts of the world (Mack and Erneberg 2002; Dehnen-Schmutz et al. 2007; Lambdon et al. 2008; Hanspach et al. 2008; Hulme 2011; Pyšek et al. 2011; Pergl et al. 2016). The exact number of species grown in cultivation worldwide, however, is not known (Khoshbakht and Hammer 2008), but recent estimates – based on the numbers of species in online garden plant encyclopaedia – indicate that at least ~70,000 species are grown in domestic gardens (van Kleunen et al. 2018a) and that ~105,000 (Mounce et al. 2017) to ~162,000 species (van Kleunen et al. 2018a) are grown in botanic gardens. This means that 20–50% of the global vascular flora is grown in cultivation and likely has been introduced outside their native ranges. Therefore, it is not surprising that 94% of the known ~13,000 naturalised species are plants

that are grown in cultivation (van Kleunen et al. 2018a). Although this does not necessarily mean that all those naturalised species escaped from cultivation, as many of them might have been introduced via other pathways, it at least suggests a prominent role of horticulture in general as a pathway for plant introductions.

Horticulture is a multi-billion-dollar industry, and the live plant imports have steadily increased in recent decades (van Kleunen et al. 2018a). Horticulture is thus still likely to be the major pathway of plant introductions. Moreover, the horticultural industry, and the fashion trends it initiates or is subjected to, makes that the introduced plants are not a random selection of the global flora. On the one hand, the origin of the introduced plants shows temporal dynamics. For example, among the woody plants brought into cultivation in Europe, the ones from Europe came mainly during the 1st wave of global spread, whereas the ones from North America and Asia came mainly during the 2nd wave of global spread (Goeze 1916). Moreover, it is likely that plants with certain characteristics are preferentially used in horticulture. Some of those characteristics promoted through horticulture, such as fast growth or long flowering duration, may also promote invasion. Furthermore, through selection and hybridisation, plant breeders created novel cultivars with their own specific characteristics. Actually, of the ~13,000 naturalised species, 219 are only known from cultivation (i.e. do not have a known native range; van Kleunen et al. 2015). Nevertheless, many of the cultivars may have reduced chances to establish in the wild, as they may be sterile or have low competitive abilities. However, efforts to specifically breed non-invasive plant cultivars are still rare (Anderson et al. 2006).

Predictions about the future developments of horticulture and their influences on the spread of alien plant species are difficult for several reasons. First, horticulture represents a large global industrial sector, and second, it is at least partly driven by fashion trends, which generates demands for certain plants or types of plants. The demand for unusual plant species has been growing continuously, and new ways of trade make it

difficult to track and control the exchange of plants. For example, more and more plants, including highly invasive ones, are now available through e-commerce (Humair et al. 2015). As e-commerce is still growing, it may represent a new major pathway of alien plant introductions in the future. The horticulture industry is constantly exploring new trends and develops new varieties, which are nowadays produced in greenhouses or laboratories instead of sampled from the field. Simply due to the sheer size of the horticultural industry, one can expect more alien plants escaping from our gardens in the future. Furthermore, due to ongoing climate change, plants that have been grown in gardens for centuries and so far have not escaped might soon find suitable climates for establishment in the wild (Haeuser et al. 2018). On the other side, public awareness of biological invasions is rising, which has in some parts of the world resulted already in shifts towards planting native species. This includes botanical gardens, which tend to plant more native species and take more care of preventing alien species from escape. However, those trends are likely too minor to counteract the rise in new introductions from the horticultural sector without implementing any further restrictions on trade and planting.

3.3.2 Management of Pathways

Target 9 of the Strategic Plan for Biodiversity (2011–2020) calls for urgent action by the CBD to identify and prioritise alien species pathways and to put in place measures to manage pathways to prevent their introduction and establishment (Hulme 2015; Saul et al. 2017). While deliberate introductions should be the most straightforward to manage, there remain major challenges to effectively address the release and escape pathways. Although robust risk assessment protocols exist for plants (Pheloung et al. 1999) and could be applied to screen the importation of all live plants, seeds, bulbs and cuttings for planting, such measures are undertaken by relatively few countries. At best, most developed nations adopt some form of blacklist of prohibited plant spe-

cies, but these are often insufficient to prevent the import of potentially invasive species (Hulme et al. 2018). Thus, opportunities for alien plants to become established through the release and escape pathways remain relatively high. Attempts to address escapes through subsequent trading bans are only effective if adopted early and without being compromised by trade or industry lobbies (Hulme et al. 2017). The management of unintentional pathways is even more challenging. Contaminants in grain are often screened under international seed testing protocols such that grain meets prescribed standards of being free from “weed” seeds, but these instruments can never be 100% effective. Certification guarantees at most 99.9% seed purity, and thus, even today, cereal seed samples can be contaminated by alien species, and given the large numbers of cereal seed sown each year, this is significant in terms of overall propagule pressure (Hulme et al. 2008).

There are stronger regulations addressing the movement of bulk soil, largely due to the risk of introducing soil pathogens rather than plant seeds. However, humans are vector of vast quantities of soil on footwear and equipment transported internationally. A single gram of soil attached to footwear can harbour as many as three seeds, and since there are over one billion international tourists worldwide each year, this represents a substantial pool of seeds being moved globally (Hulme 2015). The management of these stowaways is fairly limited; few countries take the rather severe action of the New Zealand authorities in cleaning the boots of incoming passengers. Undoubtedly, the least well understood and most weakly regulated is the natural dispersal of alien plants from one region to another through natural means. Even invasion biologists are uncertain about how to treat such species (Hulme et al. 2017; Essl et al. 2019). Natural dispersal of alien plant species can pose significant challenges to biosecurity strategies of countries if species disperse from neighbouring countries with lower standards of control (Faulkner et al. 2017). An understanding of the risks of further natural spread of alien species into neighbouring countries could be used to increase pressure (polluter pays’ principle) on the

recipient country to eradicate the alien species and even encourage cost sharing among neighbouring countries where wider benefits could be gained (Hulme 2015).

3.4 Conclusions

Plant species have been introduced by humans worldwide over thousands of years at an ever increasing rate (di Castri 1989; Seebens et al. 2017). The patterns and flows of exchange have varied in the course of time according to varying human activity, and one may expect changes in pathway importance as well. However, the relative importance of major pathways remained surprisingly stable over centuries, with introductions for ornamental purposes (including botanic gardens and other forms of horticulture) dominating throughout time as >50% of all introductions have been associated to this pathway over all waves of global spread (Fig. 3.2). As the number of alien plants and the drivers of introduction related to horticulture clearly increased during recent decades, it seems likely that trends will continue to increase also in the decades to come. The number of alien plant species is predicted to increase particularly in emerging economies with strong recent increases in economic growth such as India, South Korea, Argentina and Brazil (Seebens et al. 2015). This is a consequence of (1) a further intensification of exchange, which resulted in larger quantities of transported individuals and species; (2) ongoing land use change, resulting in higher likelihoods of establishments; and finally (3) increased source pools of native species through an ongoing integration of new exchange routes, which enables more species to enter the stages of biological invasions (Seebens et al. 2018). There might even be another wave of plant introduction and establishment as a consequence of the interacting effects of global change drivers such as climate change, land use change and global trade, which may facilitate the establishment of new plant species (Bradley et al. 2012). For individual countries with strict border controls like New Zealand or countries where biosecurity measures have been put in place

recently such as Japan, the rates of new alien species records may decrease as careful managements of pathways of alien species have the potential to distinctly reduce the number of new alien species establishments (Simberloff et al. 2013).

Addressing the challenges of containing the introduction of alien plant species requires large, global and coordinated efforts from all parties involved in this process. Although horticulture in general has been identified as the major pathway for the introduction of alien plants since centuries, it is not sufficient to just blame the horticultural industry and garden owners. An efficient mitigation of the introduction and spread of alien plants can only be achieved if all stakeholders from the general public to the industry and from local agencies to international bodies work together.

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Plant Invasions, Rising CO₂, and Global Climate Change

4

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Abstract

Although climate change and invasive species are each recognized as meaningful threats to ecological function, biodiversity, and agronomic systems, there is increasing awareness of ongoing linkages between these phenomena that will alter our understanding of their impacts. Such interactions may be of special importance regarding invasive alien plant species, as these species are likely to be directly affected by rising concentrations of atmospheric carbon dioxide (CO₂) in addition to any subsequent changes in climate, including temperature, precipitation, and extreme events. The current review is an attempt to synthesize available information related to biological interactions with CO₂ and climate change and provide, where possible, relevant case studies. In recent years, significant progress has been made in recognizing that changing climate and rising CO₂ will alter invasive alien species establishment, spread, and influence; however, it is also evident that several critical issues require additional analysis, including detection, biological integration, evolution, management, and communication.

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The purpose of this review is not to provide a final, authoritative reference but to gauge progress and provide a platform for additional inquiry. Such an inquiry should not be ignored or assimilated into traditional weed science research but rather deserves special recognition in regard to impact and management.

Keywords

Adaptation · Carbon dioxide · Climate change · Early detection · Herbicides · Invasive alien plants · Mitigation · Modeling

4.1 Introduction

At present, the global population is approaching 8 billion, likely reaching 11 billion before the end of the century. To feed, clothe, and house an ever-expanding population, plant biologists, from agronomists to plant breeders to foresters, are working tirelessly to develop a subset of the world's flora and fauna that can produce supra-natural yields when grown in monocultures. Ignoring biogeographical limits, transport, and establishment of these selected animal and plant DNAs around the world has resulted in an increasingly monotypic environment. In North America, for example, less than 10% of agricultural species are derived from native plants (Paini et al. 2016). Such intensification of international

trade has ultimately resulted in a globally homogeneous, ecological “soup,” a soup that has redefined historical perspectives of regional flora and fauna (Mooney and Hobbs 2000). Yet, the unparalleled movement of biological species is a necessary response to maximize global production of agriculturally based goods and services. For example, soybean (*Glycine max*) is not native to the United States but is, undeniably, an essential part of its economy as are crops like corn (*Zea mays*), rice (*Oryza sativa*), peaches (*Prunus persica*), and almonds (*Prunus dulcis*), as well as livestock (e.g., cattle).

While of general benefit, it is also evident that this unprecedented DNA distribution, endemic of global trade, can have negative effects. Unprecedented rates of biological introductions can lead to a small subset of species that can be extraordinarily destructive, dominating, even eliminating entire ecosystems.

The definition of such species varies. They have been referred to as “invasive,” “noxious,” “alien,” “non-indigenous,” and even “exotic” (or combinations thereof). Etymology aside, they are generally recognized as non-native or non-indigenous for a given ecosystem and whose introduction (via seed, eggs, spores, or other biological material) results in economic or environmental harm (<https://www.invasivespeciesinfo.gov/what-are-invasive-species>).

However, such definitions are not always absolute. Time and systematics can be a consideration. For example, in North America common lambsquarters (*Chenopodium album*), while originally from Eurasia, has been also found in archeological studies of native American tribes (Phillips et al. 2014) and is now considered to be a “common,” not invasive, weed.

The destructive impact of these species can also be difficult to quantify environmentally, and economic costs vary. In the United States, invasive alien species can result in damages adding up to roughly 120 billion dollars per year (Pimentel et al. 2005). In China, rapid infrastructure development is leading to a rapid dissemination (2–4 km per year) of invasive plants including *Amaranthus*, a notable agronomic weed (Horvitz et al. 2017). Lantana (*Lantana camara*), an inva-

sive vine, has spread to over five million hectares in Australia alone and poses a toxic risk for cattle (Bhagwat et al. 2012). Environmentally, the colonization and spread of water hyacinth (*Eichhornia crassipes*) and its economic impact on water availability in arid climates such as South Africa (Fraser et al. 2016) are significant. The spread of smooth Crotalaria (*Crotalaria pallida*) may drastically damage rainforest diversity in the Amazonian basin (Fonseca et al. 2006). New invasive grasses such as annual bluegrass (*Poa annua*) are also beginning to colonize Antarctica (Molina-Montenegro et al. 2014). Overall, invasive species are considered to rank second only to habitat destruction in adverse effects on ecosystem function (Wilson 2016).

Invasive species may also incur public health consequences, e.g., introduction of common ragweed (*Ambrosia artemisiifolia*) in Eastern Europe and ragweed parthenium (*Parthenium hysterophorus*) in Australia is associated with noted increases in allergic reactions, contact dermatitis, and associated asthma (McFayden 1995; Hamaoui-Laguel et al. 2015).

Without question, global trade is a primary driver of invasive species introduction and spread. However, it is also clear that rising levels of carbon dioxide (CO₂) and concomitant changes in surface temperature and climate are likely to also play a role in invasive species biology (Early et al. 2016). Such changes may be particularly relevant for plant-based invasive species as they are likely to be affected not only by temperature and climate but also directly by rising CO₂ (Ziska 2003). In addition, among invasive pests, plants (weeds) represent the greatest direct economic losses and control costs in crop production, e.g., Palmer amaranth (*Amaranthus palmeri*) (Bagavathiannan and Norsworthy 2016), as well as fire effects on rangelands, e.g., cheatgrass (*Bromus tectorum*) (Brummer et al. 2018), and water quantity or quality, e.g., hydrilla (*Hydrilla verticillata*) (Calvo et al. 2019).

Elucidation of the current and projected interactions between invasive plant biology and climate change is essential to assess the nature of the ongoing threat posed by physical and biological factors in relation to global production of food, feed, fuel,

and fiber. The goals of the current review are therefore threefold: (1) to examine the probable (recent and projected) biological links between climate/CO₂ and invasive plant species that would influence their establishment, competition, and demography, using appropriate case studies; (2) to evaluate the role of CO₂ and climate on their management; and (3) to identify research topics that require greater and immediate attention and, where appropriate, to provide recommendations that could help adapt and sustain managed systems (rangelands, agriculture, forests) in response to current and future limitations imposed by invasive plants. My aspiration in doing so is to emphasize the interactions between climate change and invasive plant biology as an understudied aspect of global ecology and to help guide future research efforts to reduce or negate these novel environmental and economic threats.

4.2 CO₂, Climate Change, and Plant Biology

As global demand for food and energy increases, fossil fuel burning and deforestation will continue to be anthropogenic sources of atmospheric CO₂. In 2018, fossil fuel-related CO₂ emissions were estimated at approximately 37.1 billion metric tons, a new record (<https://www.iea.org/geco/emissions/>). Atmospheric CO₂ concentrations are at ~410 ppm, the highest concentration in recent geological history (one million bp), approximately 45% above pre-industrial levels. At current levels of fossil fuel use and deforestation, CO₂ may exceed 800 ppm by the end of the current century (Field et al. 2014).

The rise in CO₂ will alter plant biology in two basic ways. The first reflects physical changes in the environment associated with the greenhouse trapping qualities of CO₂ and other global warming gases (e.g., CH₄, N₂O). From 1970 to 2017, global temperatures (land and ocean) increased by ~0.9 °C (Brönnimann and Wintzer 2018); global temperatures are on course for a 3–5 °C rise by 2100 (IPCC 2014). The increases in average temperature and associated temperature and weather extremes are expected to increase.

Predictions for altered precipitation are uncertain but include potential increases in drought at lower latitudes, increased precipitation at higher latitudes, and an increase in their frequency and intensity of extreme precipitation events (Rosenzweig et al. 2001; Dore 2005; Qian et al. 2011; Swain and Hayhoe 2015).

The second effect of rising CO₂ is specific to plant biochemistry. Plants evolved approximately 450 million years ago, appearing at a time when atmospheric CO₂ concentrations were between 1000 and 1200 ppm. However, since the early Miocene (about 24 million bp), CO₂ levels appear to have declined below 500 ppm (Pearson and Palmer 2000), and evidence from air sample obtained from ice core data indicate atmospheric CO₂ concentration fluctuating between 200 and 300 ppm for at least the last 800,000 years bp (Siegenthaler et al. 2005; Lüthi et al. 2008). Because CO₂ represents the sole source of carbon for photosynthesis, and because CO₂ levels have been relatively low for the recent geological past, the current increase (+29% since 1960) represents a major shift in an essential resource needed for plant growth. In addition to the direct photosynthetic effect, CO₂ can reduce stomatal aperture or frequency with concomitant increase in plant water use efficiency. Although the overwhelming majority of plant species (90 + %) lack optimal amounts of CO₂ relative to photosynthesis, i.e., those that only possess the C₃ photosynthetic pathway, the differential response among photosynthetic pathways, especially C₃ and C₄ species, is of obvious consequence in crop-weed competition. However, the role of climate change and CO₂ on agronomic weeds per se has been a focal point for other reviews (see Ziska et al. 2011; Korres et al. 2016; Chauhan 2020).

For invasive plants, the effects of CO₂ fertilization have been reported on extensively in the literature, usually at the whole plant level for managed plant systems, such as rangelands, forests, and agriculture (Kimball et al. 2002; Springer and Ward 2007; Andresen et al. 2016). Given the ubiquity of invasive plant species, evaluations have focused on both modeling or empirical aspects (Dukes and Mooney 1999; Thuiller et al. 2008; Bellard et al. 2018; Shabani et al.

2020) and experimental studies (e.g., Ziska 2003; Rogers et al. 2008; Blumenthal et al. 2016).

4.3 Overview of Climate, CO₂, and Invasive Plant Biology

While there are a number of studies specific to a given climate parameter (temperature, CO₂, inter alia), multiple interactive studies are, overall, lacking. Hence, the overview will focus on individual environmental parameters.

Extreme Weather Wind is widely recognized means for seed dispersal and establishment for weedy species, including invasive weeds such as yellow salsify (*Tragopogon dubius*), spotted knapweed (*Centaurea stoebe*), Canada thistle (*Cirsium arvense*), musk thistle (*Carduus nutans*), and others. Any increase in severe weather, particularly wind, is likely to increase seed dispersal and potential establishment of these and other invasive plants. Rising CO₂ may also indirectly affect wind and seed dispersal by increasing height or seed number (Edwards et al. 2001) with consequences for dispersal and colonization. Given the ability of some invasive plants to produce prodigious seed numbers, e.g., the invasive tree, *Ailanthus altissima*, can produce up to several million seed per year (Martin and Canham 2010); increases in wind and/or CO₂ could have a significant effect on dispersal and demography of invasive plants.

Wind is a characteristic of extreme weather events, but such events (e.g., hurricanes) are also likely to result in physical disturbance, with associated opportunities for increased germination and establishment of invasive plants. In general, invasive plants are thought to respond positively to physical disturbances (Hansen and Clevenger 2005; Leishman and Gallagher 2015) or increased resource availability (Leishman and Thomson 2005). Long-term in situ evaluations are rare; however, urban-rural microclimatic differences, endemic of near-term climate change, have resulted in a greater selection of invasive plant species (George et al. 2009).

Water While water is a recognized limitation in plant establishment, growth, and fecundity, little is known regarding altered precipitation patterns and invasive success. Blumenthal (2009) has shown that increased snowfall, or snowfall variability, may enhance the invasion of forbs in mixed-grass prairie ecosystems, with subsequent changes in range management, especially forage availability; snowfall may also be a component in the establishment of cheatgrass, a widely distributed invasive grass species in the western United States (Gornish et al. 2015).

Seed germination of rangeland invasive species such as cheatgrass or yellow starthistle (*Centaurea solstitialis*) is dependent on soil moisture. More moisture is correlated with increased overwintering rates and seed production of both species (Patterson 1995). However, both species are also drought adapted, being able to complete seed production with less water than the native plant communities. Temporal changes in precipitation patterns may also be important for invasive plant establishments. For example, increased springtime moisture associated with El Niño events may expand cheatgrass habitat (Bradley and Mustard 2005). However, a recent phylogenetic meta-analysis indicated that invasive plants tended to have a slightly more negative, but not significant, response to decreased precipitation relative to native plants (Liu et al. 2017), suggesting that precipitation per se may alter invasive plant biology and community composition, to an extent that varies depending on the species involved.

Temperature Concurrent with precipitation, temperature (soil and air) is a primary abiotic variable that can affect invasive plant biology. Temperature is a discernable factor in demographic processes including seed bank mortality, seedling survival, growth rates, and fecundity.

At present, based on a limited number of studies comparing growth responses to increased temperature between native and invasive species, no clear trends are evident. Verlinden et al. (2013) showed contrasting results between native and invasive plant pairs at an elevated temperature of +3 °C. Yu et al. (2018) indicated enhanced competitive ability of an invasive relative to a native

plant species under simulated warming conditions in a greenhouse. Sorte et al. (2013) in a meta-analysis on non-native and native species to climate change variables indicated no benefit of warmer temperatures on non-native species.

At a larger, continental scale, the probable impact of increasing temperatures favoring the distribution of invasive plants into higher altitudes (McDougall et al. 2005) or latitudes (Bradley 2010) is of obvious concern. There have been numerous studies that have used species distribution modeling or climate envelope models to project habitat shifts over large geographical scales with warming for individual and multiple invasive plant species. Some have concluded that climate, primarily temperature, will increase the area occupied by invasive alien species (Barbet-Massin et al. 2013; Gilioli et al. 2014; Kriticos et al. 2015); conversely, others have indicated a potential poleward shift in distribution but an overall reduction in area (Bradley et al. 2009; Bellard et al. 2013; Xu et al. 2013).

One of the most interesting forecasts regarding warming and an invasive alien plant was made almost 30 years ago regarding poleward migration of kudzu (*Pueraria montana* var. *lobata*) a well-recognized invasive of the southeastern United States. Sasek and Strain (1990) projected that low winter temperatures were a biological limitation to northward migration of this species, but that as winters warm, migration could be expected.

Physiology, rather than biogeography, can be a better predictor of climate-related changes in kudzu distribution (Coiner et al. 2018); nevertheless, it is also clear that since the original study (Sasek and Strain 1990), kudzu has migrated northward, concurrently with rising minimal (winter) temperatures (Ziska et al. 2011; Fig. 4.1). It is also interesting to note that a similar poleward shift has not occurred for its southernmost (Florida) occurrence. While additional information is needed, this observation is consistent with an overall increase in the area occupied by this invasive alien species.

Carbon Dioxide Current atmospheric levels are approximately 412 ppm and are expected to

increase throughout the current century under a range of emission scenarios (IPCC 2014; Franco et al. 2018). Individual studies of invasive alien plants have suggested a stronger growth stimulation, relative to naïve species, to both recent (Ziska 2003) and projected increases in CO₂ levels (Song et al. 2009). The greater response of invasive alien plants to rising CO₂ is consistent with the resource management hypothesis proposed by Blumenthal (2005, 2006) that fast-growing species that benefit from resource enhancement (e.g., more CO₂) will also benefit most from escaping natural enemies when introduced to a new environment. If so, this suggests that rising CO₂ could select for invasive relative to native plants among functionally similar species. Several studies, over a range of fumigation methodologies, e.g., the use of chambers, greenhouse, SPAR (Soil-Plant-Atmosphere-Research) units, or FACE (Free-Air Carbon Dioxide Enrichment), that have examined plant-to-plant interactions indicated preferential selection of invasive alien relative to native species with additional CO₂ (Smith et al. 2000; Hattenschwiler and Korner 2003; Dukes et al. 2011; Manea and Leishman 2011; Blumenthal et al. 2013). However, such a response is not ubiquitous (e.g., Blumenthal et al. 2016; Hager et al. 2016).

While the data arising from such methodologies are of obvious importance, especially for range management, they do not address the role of rising CO₂ specific to agronomic invasive species. That is, there are invasive alien plants that are wild relatives of widely grown crops (which are themselves non-native). In the United States, such species may include shattercane (*Sorghum bicolor*), wild oat (*Avena fatua*), and red rice (*Oryza* spp.), and because of their genetic similarity to the crop (same genus, or same genus and species) and adaptability to management practices, they are considered among the “worst” weeds for the crop. However, to date, only a few studies have compared wild and cultivated lines in this context. These studies are specific to wild and cultivated rice, where wild lines were significantly more responsive to rising CO₂ (Ziska and McClung 2008; Ziska et al. 2010).

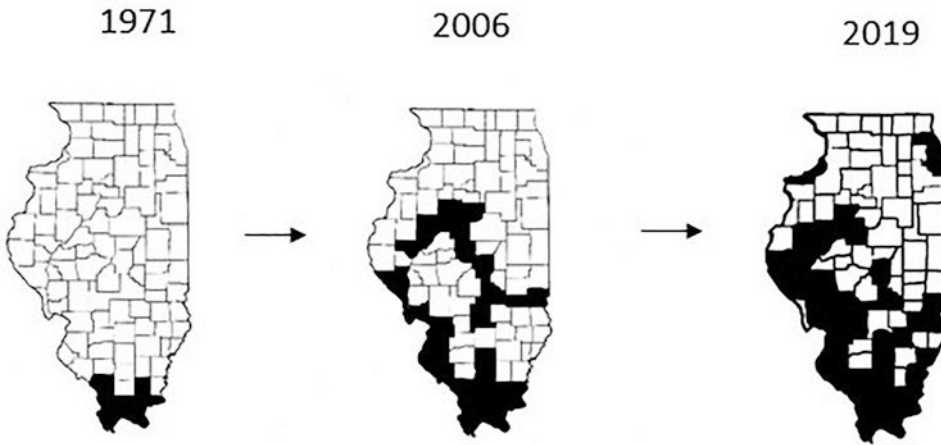


Fig. 4.1 Migration of kudzu, an invasive alien perennial for the state of Illinois since 1971. The 1971 line is from Clyde Reed, *Common Weeds of the United States*, a USDA-ARS publication. Kudzu distribution in 2006 for Illinois was estimated using three separate sources: (a) Natural Resources Conservation Service (NRCS), database of invasive US species (plants.usda.gov/java/

[profile?symbol=PUMO](https://plants.usda.gov/java/profile?symbol=PUMO)); (b) the Department of Natural Resources (DNR) for Illinois, including the publication of “The Green Plague Moves North” by the Illinois DNR; and (c) data for 2019 are from EDDMapS (<https://www.eddmaps.org/distribution/uscounty.cfm?sub=2425>)

4.4 Case Studies of Climate, CO₂, and Invasive Plants

Cheatgrass and Flammability Fire can play a significant role in rangeland ecology. Natural occurrences can facilitate nutrient cycling and promote the growth of grasses and forbs and are a natural factor in maintaining grasslands, shrub steppes, and savanna ecosystems. Fire can also be an anthropogenic tool for rangeland management.

Yet as with many environmental factors, fire frequency is critical. Too many fires can significantly reduce the growth of native grasses, forbs, and perennials with negative effects on their productivity. Cheatgrass, introduced initially from contaminated grain seed from Eurasia during the nineteenth century, can grow on poor soils, with limited rainfall. It has colonized much of the western United States, growing quickly in open spaces between perennial, native shrubs during a short rainy season. Colonization, in turn, results in a flammable “carpet” that increases fire return times from once every 50 years to once every 5 years (Whisenant 1990). As fires become more

frequent, non-adapted native species and associated ecosystems decline with cheatgrass becoming the dominant plant species. At present, it is estimated to form monocultures (>60% of the plant community) covering approximately three million acres of the intermountain west (<https://www.fs.fed.us/database/feis/plants/graminoid/brotec/all.html>).

The influence of recent CO₂ increases on cheatgrass biology has been examined. A study of three cheatgrass populations collected at different elevations from the Sierra Nevada mountain range indicated that even small 50 ppm increases in CO₂ above the pre-industrial CO₂ concentration from 270 to 420 ppm can increase the growth rate and seed production of cheatgrass while reducing its digestibility (Ziska et al. 2005). CO₂ fertilization can also alter nutritional concentration, i.e., reductions in potassium, with concomitant increases in combustibility and flammability of cheatgrass (Blank et al. 2011). Further investigation is needed, but these data suggest that CO₂ per se can increase the amount of biomass on the landscape, potentially accelerating fire frequencies, with increasing dominance of cheatgrass.

Ragweed in Eastern Europe Common ragweed is recognized globally as a primary source of human allergens associated with pollinosis and related asthma. In recent decades, its introduction and spread as an invasive alien plant species in Eastern Europe have resulted in enormous environmental and economic losses both in agriculture (as an agronomic weed) and in regard to air quality and public health (Chapman et al. 2016).

The spread of ragweed is illustrative of two processes; the first is related to socioeconomic changes. Following the collapse of communism in 1989, agricultural fields that were cooperatives were divided into smaller sections, with a renewed emphasis on mechanization, especially tillage and soil disturbance for weed management. The focus on soil disturbance, in turn, is a secondary factor in eliciting ragweed seed germination and spread (Ziska et al. 2007).

The influence of climate change on ragweed biology has been extensively examined. Changes in the first frost date in the autumn from 1977 through 2011 indicated that surface temperatures have likely lengthened both the growing season and the time of pollen exposure for common ragweed (Makra et al. 2014). Recent data from Eastern Europe have also indicated a widespread temperature-associated increase in both seasonality and pollen load from common ragweed for the fall season (Ziska et al. 2019a).

Canada Thistle and No-Till In addition to conservation benefits, the role of no-till farming for sequestering soil C has been suggested as a possible strategy for mitigating CO₂, an anthropogenic greenhouse gas. Indeed, the potential for US cropland to sequester C and mitigate the greenhouse effect has been projected to be considerable (Lal 2004). Because tillage is not used to control weeds, no-till is dependent on the use of herbicides for weed control, usually, but not limited, to preemergent applications to ensure a weed-free condition prior to planting.

However, Canada thistle is an invasive, alien plant species, often considered among the most troublesome in North America (Skinner et al. 2000; Carter and Lym 2017) and is frequently associated with no-till management (Gibson

et al. 2005). Consequently, the role of climate or rising CO₂ levels on herbicide efficacy may be essential in controlling this species for implementation of no-till management.

Initial chamber studies for Canada thistle indicated considerable photosynthetic and growth stimulation relative to both recent and projected increases in atmospheric CO₂ (Ziska 2003). For field studies of Canada thistle monocultures, elevated CO₂ stimulated belowground production (root biomass), with overall increases in the ratio of shoots to roots (Ziska et al. 2004; Ziska 2010). Consequently, the normal dose of herbicide (glyphosate) was less effective, with belowground biomass surviving and persisting, which allowed plants in the field studies to regenerate (Ziska et al. 2004). Canada thistle was grown in conjunction with “round-up ready” soybean at ambient and ambient +300 μmol mol⁻¹ CO₂ over a 3-year period using no-till cultural practices (Ziska 2010). Under these conditions, establishment of thistle increased as a function of CO₂ concentration over time even with preemergent applications of glyphosate, consistent with earlier studies regarding the role of CO₂ on herbicide efficacy for this species (Ziska et al. 2004). Although the presence of Canada thistle reduced seed yield and biomass of soybean for both CO₂ treatments, the reduction was higher for the elevated CO₂ treatment, and a significant CO₂ × Canada thistle interaction was observed. Overall, these studies suggest that under higher CO₂, selected invasive alien species, such as Canada thistle, could pose greater limitations to crop yields due to selection. Furthermore, control of such weeds, a necessary aspect of no-till management, could be impacted by CO₂-related changes in herbicide efficacy (Ziska 2016).

4.5 Climate/CO₂ and Management of Invasive Alien Species

Risk Assessment Identification and evaluation of invasive alien species remain a fundamental aspect of foreign trade. At present such evaluations are based on established protocols of

“likely” species whose invasive potential reflects similar climate regimes between exporting and importing countries (e.g., Pheloung et al. 1999). However, climate and/or CO₂ could result in dissimilar shifts in demography between regions and potentially new entry of such species. For example, as arctic ice melts, new routes for transport are likely with new introductions of invasive pest species (Nong et al. 2019). The spread of invasive pests between continents, and further range expansion because of a changing climate, emphasize the need to increase our knowledge of such species to include those which heretofore may not have been present for a specific region but are recognized globally as an economic or environmental threat. In addition, updated assessments of invasive alien species are needed. As climate changes, it is probable that new and unrecognized invasive alien species will be introduced (Petitpierre et al. 2016); conversely, other known invasive species may become less important.

Detection For the US Animal and Plant Health Inspection Service (APHIS), Natural Resources Conservation Service (NRCS), and US Forest Service (USFS), early detection and rapid response (EDRR) remain a fundamental aspect of their efforts to identify and respond to invasive plant species. The ability to assess and respond to early, nascent stages of invasion is key to eradication. The EDRR approach is used at the entry level at over 330 US airports and harbors and is also implemented in the management of invasive species (flora and fauna) in over 192 million acres of national forests and grasslands. As part of these efforts, the NRCS maintains the PLANTS database (www.plants.usda.gov), an important resource for helping private and public landowners in detecting invasive alien plants.

Models of climate induced changes in demography are also available to aid in the early detection and rapid response phase. These models use three general approaches: (a) a climate envelope approach, where geographical ranges are compared between native and introduced species to assess invasive potential (e.g., CLIMEX, Sutherst

et al. 1999); (b) evaluation and comparison of common phenological or biological traits among invasive alien plants that relate to invasive potential (e.g., Bradley 2010); and (c) a risk assessment approach that evaluates intrinsic and extrinsic factors associated with invasive success (e.g., Rejmanek 2000; Zheng et al. 2018).

Remote sensing of invasive alien plants offers a unique and potentially effective tool to identify the occurrence and temporal colonization of terrestrial and aquatic invasive plants (Lawrence et al. 2005; Santos et al. 2009). As reviewed by Vaz et al. (2018), remote sensing was used primarily to map invasive alien plant species. However, by the mid-2000s, due to increasing technological advances, remote sensing could also aid in the prediction of early invasion stages and evaluation of their impacts. Such improvements could be used to help in current geospatial modeling efforts as well as determining colonization and invasion dominance over time (Vaz et al. 2018).

Biological Control Biological control of invasive alien plants is likely to be impacted by climate and/or rising levels of CO₂. Such impacts may reflect climate variability (temperature, precipitation) and dissimilar biological responses between the biocontrol agent and the invasive species (Hellmann et al. 2008). Direct CO₂ effects could also result in qualitative changes in the host plant (e.g., increases in the C:N ratio), with subsequent effects on biocontrol efficacy. Overall, loss of synchrony between the development and reproduction of potential biocontrol agents and invasive alien plant species is likely to occur with climatic change.

Empirically, climate and CO₂ are likely to alter biological control of invasive pests. For example, in transgenic *Bacillus thuringiensis* (Bt) cotton (*Gossypium hirsutum*), elevated CO₂ reduced Bt protein production relative to the ambient CO₂ condition (Coviella et al. 2000). Conversely, recent work with *Candida sake* CPA-1, a biocontrol agent of fungal pathogens, indicated that elevated CO₂ could improve establishment of viable populations of this agent. Other work related to *Agasicles hygrophila*, a

biocontrol agent of alligator weed (*Alternanthera philoxeroides*), an invasive aquatic weed, indicated that the efficacy of *A. hygrophila* could be increased when alligator weed was grown at higher CO₂ concentrations (Shi et al. 2019), whereas stem galling moth's (*Epiblema strenuana*) ability to control *parthenium* (*Parthenium hysterophorus*) was unaffected by CO₂ concentration (Shabbir et al. 2019). Similarly, change in climate, esp. temperature and rainfall, may optimize or negate other biocontrol measures for invasive plant species (Seastedt 2015). Assessing biocontrol efficacy is an essential part in evaluating current efforts but is also necessary to identify and facilitate appropriate biological control.

Physical Control One ubiquitous means of controlling invasive plant species (and other weeds) is physical removal via hand weeding, animal grazing, or by mechanical means. At present, studies evaluating how climate and rising CO₂ alter physical management of invasive plants have not been conducted. Yet, observations based on available data suggest that physical control would be affected. For example, rising CO₂ can alter root: shoot ratio with greater root or rhizome growth of perennial weeds, including invasive species, with subsequent effects on increasing asexual reproduction (e.g., Rogers et al. 1994, 1995; Ziska 2003). Assuming belowground material (roots, tubers, etc.) can regenerate whole plants; mechanical practices such as plowing could, potentially, help spread invasive plants.

Chemical Control If an invasive species is widely established in a natural environment, then chemical control is an ineffective management technique. However, in agroecosystems, herbicide application, particularly in developed countries (e.g., United States, Canada, Australia, and Japan), is among the most widely used plant management strategies, even for invasive alien plants (Ziska 2016). To date there have been several studies that have evaluated the role of cli-

mate and CO₂ on changes in herbicide efficacy. Such studies have, in general, revealed negative impacts of changing climates and CO₂ levels on herbicide efficacy (Manea et al. 2011; Jugulam et al. 2018; Waryszak et al. 2018), but there are exceptions (e.g., see Jabran and Dogan 2018).

Climate is already recognized as a factor affecting application uniformity and herbicide placement. It is anticipated that changes in precipitation (either as a single extreme event or higher averages) could dilute the active ingredient of the herbicide, exacerbate leaching, and increase groundwater contamination (e.g., Froud-Williams 1996; Carere et al. 2011). Similarly, windy conditions could increase drift risk. Higher temperatures both could increase herbicide effectiveness via increased absorption and translocation and could enhance their volatility. Overall, increased climatic uncertainty could influence the timeliness of applications, spray coverage, volatilization, movement, and accidental injury associated with herbicide application (Ziska 2016).

In addition to abiotic changes, climate and CO₂ could also directly affect plant biochemistry. Rising CO₂ or temperature can affect photosynthesis, enzymatic activity, and pigment production, potential sites of action for several herbicides including atrazine, amitrole, and glufosinate. As such, additional CO₂ or warmer temperatures could, by promoting growth, increase the efficacy of these herbicides. Conversely, other aspects of rising CO₂, e.g., the ubiquitous effect on reducing protein levels in a wide range of plant tissues (Taub et al. 2008; Loladze 2014), could result in less demand for aromatic and branch chain amino acids, with a potential decline in the efficacy of herbicides that act as inhibitors of amino acid biosynthesis (e.g., glyphosate; Varanasi et al. 2016). Additional information regarding potential physiological interactions (e.g., metabolic resistance) and the consequences for herbicide efficiency will be necessary to fully evaluate CO₂ and climate consequences.

4.6 Uncertainties, Recommendations, and Critical Needs

Detection and Forecasting Expanding global trade, exchange of new species across environmental regions, and a changing climate all contribute to increased uncertainty as to the distribution of current and potential invasive pests. While land managers possess a historical working knowledge of pest pressures (including invasive species), rates of change in demography may necessitate enhanced monitoring and assessment of new invasive threats.

How can monitoring be improved? Geographical identification is an obvious means to quantify invasive pest establishment and spread and is becoming more available. One such tool is the Early Detection and Distribution Mapping System (www.EDDMapS.org), based out of the Center for Invasive Species and Ecosystem Health at the University of Georgia. EDDMapS tracks and records distribution of a wide range of invasive species across the United States. It synthesizes data from public and private sources that are integrated to create a national invasive species database. However, it is a static database. While providing up-to-date assessments, it does not provide a sense of historical change—when was the invasive first observed? How quickly is a new invasive spreading?

These are not theoretical questions. Spotted lanternfly (*Lycorma delicatula*) was first discovered in Berks county Pennsylvania in 2014 and, as of 2019, was extending its range to upstate New York (Weigle et al. 2018). It threatens products from wine to apples and from forests to craft beer, with an estimated damage cost of approximately \$18 billion USD in Pennsylvania alone. Invasive plants are less mobile and may spread more slowly than animal invaders but may readily escape notice in the process. Invasive strains of Phragmites (*Phragmites australis*), for example, were found to expand rapidly during the 1990s (Chambers et al. 1999). Recent floods in the Midwest may also result in opportunities for invasive alien plant colonization, including Phragmites (<https://www.thefencepost.com/>

[news/invasive-plants-to-look-for-after-the-flood/](#)). Improving detection to assess migration rates of invasive species is key in preparing for their impact.

In addition, while invasive databases are available, they are for the most part country specific. Data sharing would be crucial in evaluating invasive pest threats in real time. For example, warmer winters have facilitated the northward migration of mountain pine beetle (*Dendroctonus ponderosae*) (Bentz et al. 2016). Around 2007–2011, it crossed over the Rocky Mountains into continuous boreal forest extended to eastern Canada. However, the rate of spread, and likely introduction into northeastern forests in the United States, is unclear.

Given the global increase and availability of social media, it seems reasonable to leverage citizen science observations into an appropriate data sharing platform that could inform growers and land managers as to occurrence, colonization, and threat assessment of invasive pests in real or near real time. As pest threats become more global through increased trade, such a platform could help to increase and coordinate detection efforts on a global basis. Preemptive monitoring in areas altered by climate change in ways likely to facilitate invasive habitat would also be a useful means for detecting new invasives and their subsequent eradication (Leishman and Gallagher 2015). In addition, field and socioeconomic surveys are important to assess the actual invasive range, spread, and mode of dispersal and impacts.

Biological Integration Science is often reductionist in nature, focusing on isolating and studying the impact of a single variable within a single plant species. However, climate change reflects multiple interactions and drivers on invasive alien plant biology from drought to temperature to elevated CO₂ (Leishman and Gallagher 2015). Consequently, it becomes necessary to “scale up” from the plot level (with one or two variables) to a geospatially significant area with multivariable interactions. However, there are methodological difficulties in studying multi-trophic interactions for long-term periods; consequently, models are

frequently used to determine species dynamics and demographics in relation to climatic change for geographically relevant regions.

Additional efforts are needed to look at interactions among multiple climate change effects, including CO₂ interactions with temperature or drought, or multiple species assessment. Such efforts promise to integrate concurrent climatic change effects and provide mechanistic information crucial to model improvement. Such information may reflect an integration of important aspects, from seed bank dynamics (Leishman et al. 2000), to competition, to herbivory, etc. that are not always included in current modeling efforts. Overall, data sharing and data synthesis between experimentalists and modelers are needed to avoid a fragmented, selective data base.

Evolution and Selection While incomplete, there is increasing empirical evidence for rapid micro-evolutionary change within agronomic and invasive weed species (Neve et al. 2009; Moran and Alexander 2014). Such evolutionary potential is perhaps best illustrated by the rapid and widespread documentation of herbicide resistance (Heap 2014).

Regarding invasive alien species, considerable effort has gone into understanding the role of evolution following their introduction into new territory. Release from specialist herbivores in their introduced range has been suggested to allow for evolution of reduced defense and increased growth and/or competitive ability (Blossey and Notzold 1995). Common garden studies support this hypothesis, indicating that rapid evolution in growth and defense is relatively common in introduced ranges (Blossey and Notzold 1995; Felker-Quinn et al. 2013; Zhang et al. 2018). It is possible that the traditional paradigm of invasive evolution as a slow process is incomplete and that rapid evolutionary change (years or decades) could also include evolution in response to climate (e.g., Ravet et al. 2018; Ziska et al. 2019b). However, direct evidence of weed evolution in response to climate change is rare. Seminal studies (e.g., Franks et al. 2007; Franks 2011) using the annual weed *Brassica rapa* collected before and after a severe drought indicated

that this species responded to selection by evolving earlier flowering and lower water use efficiency (a drought escape strategy) within just a few generations. Similarly, 13 years of experimental drought appear to have led to evolution of drought escape in the common weed, *Plantago lanceolata* (Ravenscroft et al. 2015). Overall, several specific biological questions related to climate-induced shifts in evolution, including mutation rates, the role of epigenetics, hybridization, selection of resistant vs. sensitive herbicide biotypes, etc., remain unanswered in regard to invasive plant species.

Management Without question, there are several managerial aspects, from the biological to the chemical, likely to be altered by rising CO₂ levels and climate uncertainty. For the United States, where chemical control dominates but at present is facing unprecedented levels of herbicide resistance (Duke and Heap 2017), the role of climate or CO₂ in selection, especially between resistant and sensitive biotypes, is fundamental. Recent evidence indicates that herbicide-resistant biotypes of junglerice (*Echinochloa colona*), an invasive weed of rice fields in the southern United States, may be selected by rising CO₂ and/or higher temperatures (Refatti et al. 2019; Fig. 4.2). There are many questions still to be answered, e.g., How will herbicide application rates change with climate? What are the consequences for increased resistance for chemical control of invasive or native weed species?

If chemical management becomes less effective, how can land managers compensate, given past reliance on chemical control measures? Do we need to develop new chemical control measures? For biological management, will differential responses to climate change or CO₂ alter predator-prey relationships? Will cultural management (e.g., flooding in rice) be affected by climate-induced changes in water availability? Should greater attention be given to restoration of native habitats around agricultural fields or managed rangelands to prevent or minimize invasion? Is there a role for integrated pest management (IPM) with uncertain climates? If so, how does climate alter IPM guidelines?

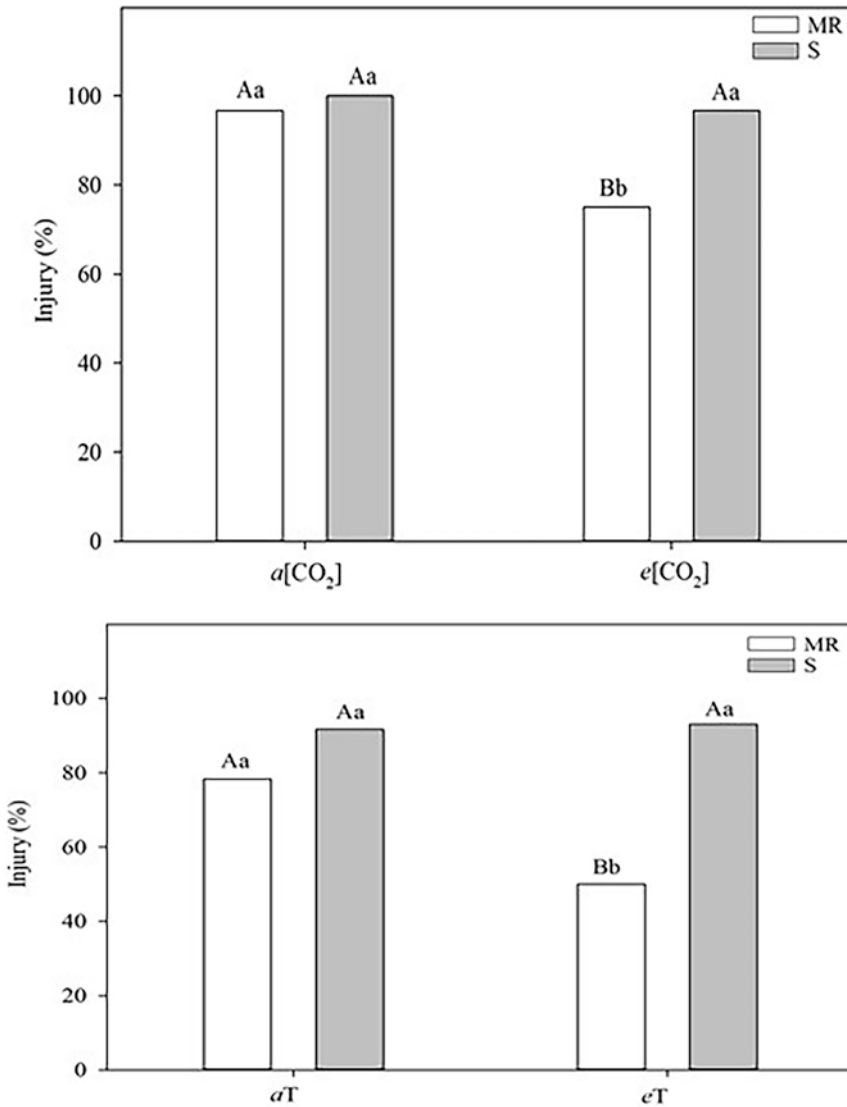


Fig. 4.2 Differential effects of herbicide application on multiple-resistant (MR) and susceptible (S) biotypes of jungle rice (*Echinochloa colona* L.), 7 days after treatment. Note the reduction in efficacy at warmer temperatures and higher CO_2 levels for the MR biotype. Adapted

from Refatti et al. 2019. The x-axis for the top figure consists of $\alpha[\text{CO}_2] = 400 \pm 50 \mu\text{mol}\cdot\text{mol}^{-1}$; $e[\text{CO}_2] = 700 \pm 50 \mu\text{mol}\cdot\text{mol}^{-1}$; the x-axis for the bottom figure consists of $\alpha T = 23/35^\circ\text{C}$ (night/day); $eT = 26/38^\circ\text{C}$ (night/day)

Given the potential for rapid climatic change, and the acknowledged role of rising CO_2 on invasive alien species biology, a reassessment of invasive management techniques to accelerate testing, pinpoint vulnerabilities, and adopt, through experimentation or modeling, new approaches will be necessary.

Communication While the research challenges are recognized, the complexity and, at times, conflicting interactions among long-term climate, short-term weather, differential stimulation of plant growth and reproduction by CO_2 , dynamics between concurrent climatological variables, and impact assessments can lead to uncertainties

even among invasive species experts. It is to be expected, therefore, that the impacts of invasive species and the implications of climate and CO₂ on their impacts and management may be completely unknown to policy makers and other non-experts. Consequently, the ability of scientists to relate their findings to pragmatic needs in straightforward, understandable language is essential to provide information to interested parties, from land managers to policy makers.

The proliferation of social media and the internet has had profound impacts on communication, including between scientists, policy makers, and the public. Unquestionably, it has provided opportunities for mass communication and for reaching and educating stakeholders. However, the interaction between science, climate, and invasive species is challenged by multiple channels and platforms that undermine public understanding, with all factual aspects of climate change contested depending on the political or economic agenda. Effort is needed to improve information regarding climate, CO₂, and invasive alien plant biology and impacts. Debates on impacts must incorporate both the evidence presented and underlying rationale.

Finally, from a communications standpoint, there is a need for increased inclusion of invasive pest (flora and fauna) threats into global change projections. The difficulty of assessing such threats in the context of agronomic or ecosystem impacts is acknowledged; however, climate change and invasive alien species should not be viewed in isolation. While progress is being made (e.g., <https://nca2018.globalchange.gov/chapter/7/>), the temporal onset of climatic uncertainty indicates greater focus on invasive biology, particularly at the global modeling level.

4.7 Conclusions

Invasive alien plant species are a well-recognized existential threat to agricultural and natural lands. Infestation of forests and rangelands, constraints on agricultural productivity, negative consequences for riparian systems, and elimination of native biodiversity are widely acknowledged. As

trade volume continues to increase with new international connections, the pressures from invasive species will only intensify.

As this review and others (Hellmann et al. 2008; Leishman and Gallagher 2015; Early et al. 2016; Paini et al. 2016) reveal, there is an undeniable consequence of climate change and rising CO₂ in altering, and potentially exacerbating, invasive species destructive effects. There are sound empirical links between climate and CO₂ specific to invasive species biology, from establishment to competitive interactions to chemical management, to support probable interactions.

At present, experimental data are minimal, and projected models are incomplete. The complexities of invasive species and CO₂/climate are defined more by unknowns than what has been reported. To that end, critical needs and uncertainties are provided here, but it should be stressed that these are, by no means, inclusive. Rather, it is hoped that the current assessment merely represents a starting platform for additional research and communication efforts that will concentrate on a complex, multifaceted scientific challenge whose solution will be essential in preserving wildlife and human well-being.

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Plant Invasions in Asia

5

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Abstract

Asia, occupying nearly 30% of the earth's terrestrial surface, is one of the most important continent known for its highly diverse culture, economy, geography, and ecology. Three of the world's five largest economies, and nearly two-thirds of the world's population, are in Asia. The continent has a diverse range of habitats including tropical moist and boreal for-

ests, deserts, and the Arctic tundra. Eleven out of 36 global biodiversity hotspots are in Asia, all of which are threatened due to multiple human-mediated drivers including biological invasions. The number of known invasive alien plant species (IAPS) currently present in Asia is high, and their number and distribution are expected to increase further due to a lack of effective management responses, land use and climate changes, and expanding international trade, travel, and transport. IAPS such as *Ageratina adenophora*, *Chromolaena odorata*, *Lantana camara*, *Leucaena leucocephala*, *Mikania micrantha*, *Mimosa diplotricha*, *Parthenium hysterophorus*, and *Pontederia crassipes* are widespread in the tropical and subtropical regions of Asia. Most of the known IAPS in Asia have a Central and South American origin. However, information on biological invasions, especially those of plants, is poor and fragmented, hampering efforts to develop and implement policies and management interventions. The continent is lagging behind much of the world in research effort and knowledge generation related to plant invasions. Capacity, both human and otherwise, of most countries to address biological invasions is low. Most countries (particularly in Central Asia) also lack a comprehensive database of IAPS. Ecological impact studies are also lacking in Southeast, Central, and North Asia. With a few exceptions, the eco-

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conomic cost of plant invasions is also unknown in most countries. Priority actions required for effective management of IAPS in Asia include regional collaboration for research and knowledge sharing, promotion and institutionalization of biological control, and increased focus on socioecological research related to plant invasions. Additionally, efforts are required at the continental scale to make all stakeholders aware of the problem of plant invasions for the formulation of appropriate policies and implementation of effective management strategies.

Keywords

Distribution · Diversity · Global change · Impacts · Invasive alien species · Management · Native range · Policy

5.1 Introduction

Asia is the world's largest continent and occupies nearly 30% of the terrestrial surface on earth. The continent is physically, biologically, economically, and culturally diverse, rising from below sea level (South Caspian Sea plains in northern Iran) to the highest peak in the world, Mt. Everest (8849 masl). Twelve of the 20 largest countries by population are in Asia, with China (1.4 billion) and India (1.3 billion) being the most populous (www.worldometers.info/world-population/). Other countries have very high (e.g., Singapore, Bangladesh, South Korea, Philippines) to very low population densities (e.g., Mongolia, Kazakhstan, Russia, Turkmenistan). Among the world's five largest economies, three are in Asia (China, Japan, and India) (<https://www.worldometers.info/gdp/gdp-by-country/>).

Ecologically diverse ecosystems including equatorial tropical rainforests, hot deserts, cold and hot arid steppe, and boreal forests occur in Asia. Eleven of the 36 Global Biodiversity Hotspots are located in Asia: two in East Asia, three in each of Southeast and South Asia, two in West Asia, and one in Central Asia (Mittermeier et al. 2011; Critical Ecosystem Partnership Fund, www.cepf.net/node/4422). The continent also

has 5 (China, India, Indonesia, Malaysia, Philippines) of the 17 most mega-diverse countries in the world. Out of 238 global ecoregions of conservation priority, more than 50 terrestrial and freshwater ecoregions (out of 195 globally) are present in Asia (Olson and Dinerstein 2002).

The higher number of biodiversity hotspots in Asia (Mittermeier et al. 2011) suggests that the continent is not only rich in biodiversity, including endemic species, but is also witnessing a rapid loss of primary natural habitats. As elsewhere in the world, the rich biodiversity and natural environment of Asia have been threatened due to anthropogenic activities including biological invasions (IPBES 2018). A large number of alien plant species have already naturalized in different regions of the continent (Sect. 5.2), with many of them inflicting detrimental impacts on the environment and economy (Sect. 5.5). The national response capacities of most of the countries in Asia (except China and Japan) to address emerging risks associated with biological invasions are poor compared to some countries in North America, Western Europe, and Oceania (Early et al. 2016). This situation may lead to an increase in the number of invasive alien species (IAS) and their impacts in the future (Paini et al. 2016; Seebens et al. 2015). Many Asian countries are lagging in terms of research efforts and knowledge generation, which might contribute, along with other factors, to inadequate management and policy responses to plant invasions (Sect. 5.6).

In this chapter, we review the diversity and distribution patterns of invasive alien plant species (IAPS) across the major regions and countries in Asia, their biogeographic origin, and introduction pathways, impacts on environment and socio-economy, and management approaches including policy responses. We also highlight knowledge gaps and prospects for future research to improve the knowledge base for informed management and policy decisions. We use the terms such as “alien,” “casual,” “naturalized,” and “invasive” species following the definition given by Pyšek et al. (2004). Considering physical and biological variation, and for ease of presentation, we divide the continental Asia into six regions: East (6 countries), Southeast (11), South

(8), West (16), Central (5), and North Asia (Russia).

5.2 Diversity

The number of alien species is continuously increasing worldwide, without any sign of abatement (Seebens et al. 2017). Increasing movement of people and goods has dramatically increased the number of organisms being moved around the world, many of which have established and proliferated outside of their native range. The key factors that determine the number of alien species at national or regional levels are per capita gross domestic product, population density, and percentage of lands used for agriculture (Essl et al. 2019). Based on available data, the numbers of naturalized plant species currently present in Asian countries are relatively low compared to countries in Western Europe and North America (van Kleunen et al. 2015), but the scenario is most likely to change in the near future because South and East Asian countries (India, South Korea, Thailand, and China) are expected to witness the highest increase in absolute number of naturalized species in future with their expanding global trade and economic growth (Seebens et al. 2015). Generally, with a very few exceptions, Asian countries lag far behind in generating biodiversity-related information (Meyer et al. 2016), which obviously includes data on the occurrence and distribution of alien species. Some countries in Asia are yet to produce national checklists of IAS. Recently, the Global Register of Introduced and Invasive Species (GRIIS), with technical help from scientists working in respective countries, compiled country-wide lists of introduced and invasive species across the world (Pagad et al. 2018). Despite the lack of capacity and resources, especially in developing countries in Asia, to develop comprehensive lists, we have used this database to reflect the state of plant invasions in countries for which information on diversity of naturalized plant species is lacking. We are also conscious of the fact that the GRIIS database may have errors because data providers often used the terms casual, naturalized, and

invasive interchangeably. For example, the number of naturalized plant species reported for the small island nation Maldives (area ~300 km²) in South Asia is 203, which is high compared to Pakistan (area ~881,912 km²), the second largest country in the same region, which has been reported to have only 141 naturalized plant species (Table 5.1). Similarly, 2061 species are included in the GRIIS database for India, which is significantly higher than the 471 naturalized and IAPS recorded by Inderjit et al. (2018). It seems that for many countries, the GRIIS database has also incorporated those alien species, which are currently cultivated and have not escaped into the wild, or included agriculture weed species of native origin, which has led to the higher number. In essence, the major problem with documentation of IAPS is the non-uniform adoption of standard definitions of alien, casual, naturalized, and invasive species by different workers, which leads to either over- or underestimation of species numbers (Khuroo et al. 2011a, 2012a).

5.2.1 East Asia

East Asia covers about 11.9 million km² with a combined population of *ca.* 1.6 billion people. The countries in this region include the People's Republic of China (China), Japan, Mongolia, the Democratic People's Republic of Korea (North Korea), and Republic of Korea (South Korea). Considered as regions or provinces, Hong Kong, Macau, and Taiwan were included in the data set for China. Owing to wide-ranging geographical and ecological conditions, East Asia has many naturalized plant species, especially China, and the risk is ever-increasing through cross-border trade and travel. China has 861 naturalized plant species (Jiang et al. 2011) of which 324 species are invasive (Axmacher and Sang 2013; Shen et al. 2018). Families with the most IAPS are the Asteraceae (60 species), Poaceae (42), Fabaceae (28), and Brassicaceae (22). Major IAPS in China include *Alternanthera philoxeroides*, *Ambrosia artemisiifolia*, *Ageratina adenophora*, *Pontederia crassipes*, *Mikania micrantha*, *Solidago canadensis*.

Table 5.1 Number of naturalized species reported from Asian countries. The data extracted from GRIIS database (www.griis.org) on September 2019, except otherwise indicated. Data for Lebanon is not available (NA)

Region and country	Area (km ²) ^a	Number of naturalized plant species
<i>East Asia</i>		
China	9,708,095	861 ^b
Japan	377,930	1542
Mongolia	1,564,110	35
North Korea	120,538	243
South Korea	100,210	499
Taiwan	36,193	627
<i>Southeast Asia</i>		
Brunei	5765	110
Cambodia	181,035	125
Indonesia	1,904,569	651 ^d
Laos	236,800	250
Malaysia	330,803	287
Myanmar	676,578	117
Philippines	342,353	345
Singapore	710	532
Thailand	513,120	131
Timor-Leste	14,874	412 ^f
Vietnam	331,212	243
<i>South Asia</i>		
Afghanistan	652,230	56
Bangladesh	147,570	107
Bhutan	38,394	244
India	3,287,590	471 ^c
Maldives	300	203
Nepal	147,181	179
Pakistan	881,912	141
Sri Lanka	65,610	115
<i>West Asia (Middle East)</i>		
Bahrain	765	11
Cyprus	9251	341
Iran	1,648,195	118
Iraq	438,317	53
Israel	20,770	196
Jordan	89,342	69
Kuwait	17,818	12
Lebanon	10,452	NA
Oman	309,500	24
Qatar	11,586	8
Saudi Arabia	2,149,690	82
State of Palestine	6220	11
Syrian Arab Republic	185,180	30
Turkey	783,562	228 ^e
United Arab Emirates	83,600	29

(continued)

Table 5.1 (continued)

Region and country	Area (km ²) ^a	Number of naturalized plant species
Yemen	527,968	208
<i>Central Asia</i>		
Kazakhstan	2,724,900	15
Kyrgyzstan	199,951	5
Tajikistan	143,100	7
Turkmenistan	488,100	6
Uzbekistan	447,400	7
<i>North Asia</i>		
Russia (including European Russia)	17,098,242	956

^a<https://www.worldometers.info/geography/largest-countries-in-the-world/>, accessed on 25 January 2020

^bJiang et al. (2011)

^cInderjit et al. (2018)

^dTjitrosoedirdjo (2005)

^eUludag et al. (2017)

^fWestaway et al. (2018)

sis, *Flaveria bidentis*, and *Spartina alterniflora* (Wan et al. 2017). In Japan, 1552 alien species of vascular plants are naturalized (Mito and Uesugi 2004), of which 149 species are invasive (NIES 2019). The most species-rich invasive plant families are the Asteraceae (40 species), Poaceae (18), Fabaceae (9), and Scrophulariaceae (8). The most frequently reported IAPS occurring in riparian zones of Japan include *Solidago altissima*, *Robinia pseudoacacia*, *Erigeron canadensis*, *Paspalum distichum*, and *Sorghum halepense* (Miyawaki and Washitani 2004).

According to Jung et al. (2017), there are 320 alien plant species belonging to 181 genera and 46 families in South Korea with Poaceae (75 species), Asteraceae (63), Fabaceae (22), and Brassicaceae (20) being the most species-rich families. The most widely distributed species are *Phytolacca americana*, *Amorpha fruticosa*, *Robinia pseudoacacia*, *Trifolium repens*, *Ambrosia artemisiifolia*, *Bidens frondosa*, *Erigeron canadensis*, *E. annuus*, *Galinsoga quadriradiata*, and *Taraxacum officinale*. In North Korea, 226 alien plant species belonging to 162 genera and 64 families have been recorded (Son et al. 2009). Families with a high number of alien plants are Asteraceae (29 species), Fabaceae

(22), Poaceae (18), and Solanaceae (11). *Ambrosia artemisiifolia*, *Galinsoga parviflora*, and *E. canadensis* were prioritized for management due to their high invasiveness (Son et al. 2009). According to Kim and Kil (2016), South and North Korea combined (i.e., Korean Peninsula) have 504 alien plant species, of which 48 (9.5%) are invasive. In Mongolia, 51 IAPS belonging to 48 genera and 23 families are reported with the most species-rich families as Poaceae (8 species), Fabaceae (7), and Asteraceae (6) (Urgamal 2017). Based on the available data, China has the highest number of IAPS in East Asia, followed by South Korea, North Korea, Japan, and Mongolia.

5.2.2 Southeast Asia

Southeast Asia includes Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Singapore, Philippines, Timor-Leste, Thailand, and Vietnam. The region is geographically south of China, east of the Indian subcontinent, and northwest of Australia. Current knowledge of invasive alien species in many countries in this region is largely based on anecdotal evidence (Peh 2010). This finding is supported by a study in the Lower Mekong Basin where it was found that there was a lack of information on the spread and impacts of invasive species in Cambodia, Lao PDR, Thailand, and Vietnam (MWB and RSCP 2006). Available databases, mainly GRIIS (2019), and literature surveys revealed that Indonesia has the highest number of naturalized plants with 651 species, followed by Singapore (532 species) and Timor-Leste (412), with the lowest number in Brunei (110) (Table 5.1). Many of these naturalized species are invasive in the region. A review by Nghiem et al. (2013) revealed that there were 151 IAS in the region of which 75 were plant species, with the highest number of IAPS recorded from the Philippines (34), followed by Indonesia (32), Singapore (26), and the lowest number in Brunei (5). Two IAPS, *Lantana camara* and *Leucaena leucocephala*, have been reported in all 11 Southeast Asian countries while *Chromolaena*

odorata and *Pontederia crassipes* from 10 countries of this region (Table 5.2).

In the Global Compendium of Weeds, Randall (2012) recorded 2150 weed species in Southeast Asia. In comparison, Waterhouse (1993) listed 232 major weed species of which 140 were highly important and 63 were believed to be alien. According to Randall (2012), only 95 species could be regarded as IAPS in Indonesia, followed by 38 in Vietnam and 32 in Cambodia. The species shared by at least ten countries in the region include *C. odorata*, *P. crassipes*, *Eleusine indica*, *L. leucocephala*, *L. camara*, *Mimosa pudica*, *Pistia stratiotes*, *Psidium guajava*, and *Scoparia dulcis*. Witt (2017) only lists 56 IAPS as posing the biggest threat to biodiversity and livelihoods in the region, which seems to be an underestimate, and lists 5 aquatic species (e.g., *P. crassipes*, *Salvinia molesta*), 3 grasses (e.g., *Brachiaria mutica*, *Cenchrus echinatus*), 9 climbers (e.g., *Mikania micrantha*, *Passiflora foetida*), 11 herb species (e.g., *Parthenium hysterophorus*, *Sphagneticola trilobata*), 13 shrub species (e.g., *C. odorata*, *L. camara*), 2 succulents (e.g., *Jatropha gossypifolia*), and 13 tree species (e.g., *L. leucocephala*, *Mimosa pigra*).

There are a number of country reviews although many of these appear to be rather incomplete such as for Brunei and Cambodia, while other countries (e.g., Indonesia, Singapore) have more detailed information. In a review by Tamit (2003), no IAPS was reported for Brunei, with five being reported by Nghiem et al. (2013) 10 years later. Cambodia's Sixth National Report to the Convention on Biological Diversity states that "information on invasive alien species in forest ecosystems in Cambodia is very limited" and mentioned the occurrence of 13 IAPS with *M. pigra*, *Mimosa diplotricha*, *C. odorata*, and *M. micrantha* as being particularly problematic (Department of Biodiversity 2019). In Indonesia, Tjitrosoedirdjo (2005) reported the presence of 1,936 alien plant species belonging to 87 families with Asteraceae (162) and Poaceae (120) being the most speciose families. Approximately one-third (651 species) of the total alien species listed are either naturalized or agricultural weeds. The

Table 5.2 Countries of occurrence of the 21 IAPS (included in the 100 among the world's worst invasive species, Lowe et al. 2000) in different regions of Asia. North Asia has been excluded from the table because none of the listed species have been reported from that region

SN	Name of species	Regions in Asia				
		East Asia	SE Asia	South Asia	West Asia	Central Asia
1	<i>Acacia mearnsii</i>	China, Japan	Indonesia, Vietnam	India, Pakistan, Sri Lanka	–	–
2	<i>Cecropia peltata</i>	–	Malaysia	–	–	–
3	<i>Chromolaena odorata</i>	China, Taiwan	Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand, Vietnam	Bangladesh, Bhutan, India, Nepal	–	–
4	<i>Cinchona pubescens</i>	–	–	India, Sri Lanka	–	–
5	<i>Clidemia hirta</i>	Japan, Taiwan	Brunei, Malaysia, Singapore, Thailand, Vietnam	India, Sri Lanka	–	–
6	<i>Lantana camara</i>	China, Japan, Taiwan	Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand, Timor-Leste, Vietnam	Afghanistan, Bangladesh, Bhutan, India, Maldives, Nepal, Pakistan, Sri Lanka	Cyprus, Iran, Israel, Palestine, Saudi Arabia, Turkey, Yemen	–
7	<i>Leucaena leucocephala</i>	China, Japan, Taiwan	Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand, Timor-Leste, Vietnam	Bangladesh, Bhutan, India, Maldives, Nepal, Pakistan, Sri Lanka	Bahrain, Cyprus, Iraq, Iran, Israel, Lebanon, Saudi Arabia, Yemen	–
8	<i>Melaleuca quinquenervia</i>	China	Malaysia, Thailand, Vietnam	India	–	–
9	<i>Miconia calvescens</i>	–	–	Sri Lanka	–	–
10	<i>Mikania micrantha</i>	China, Taiwan	Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand, Vietnam	Bangladesh, Bhutan, India, Nepal, Sri Lanka	–	–
11	<i>Mimosa pigra</i>	Taiwan	Brunei, Cambodia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand, Vietnam	India, Sri Lanka	–	–
12	<i>Opuntia stricta</i>	China, Taiwan	Vietnam	India, Nepal, Sri Lanka	Yemen	–
13	<i>Pinus pinaster</i>	Japan	–	–	–	–
14	<i>Pontederia crassipes</i>	China, North Korea, Japan, South Korea, Taiwan	Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Philippines, Singapore, Thailand, Vietnam	Bangladesh, Bhutan, India, Maldives, Nepal, Pakistan, Sri Lanka	Iran, Iraq, Israel, Jordan, Lebanon, Palestine, Syria, Turkey	–
15	<i>Prosopis glandulosa</i>	Japan	–	India, Pakistan	Iran, Israel	–

(continued)

Table 5.2 (continued)

SN	Name of species	Regions in Asia				
		East Asia	SE Asia	South Asia	West Asia	Central Asia
16	<i>Psidium cattleianum</i>	China	Malaysia	–	–	–
17	<i>Salvinia molesta</i>	China, Japan, Taiwan	Indonesia, Malaysia, Philippines, Singapore, Thailand	Bangladesh, India, Pakistan, Sri Lanka	Israel	–
18	<i>Spartina anglica</i>	China, North Korea, South Korea	–	–	–	–
19	<i>Spathodea campanulata</i>	China, Taiwan	Laos, Malaysia, Philippines, Singapore, Thailand	Maldives	–	–
20	<i>Sphagneticola trilobata</i>	China, Japan, Taiwan	Malaysia, Singapore, Thailand	India, Maldives, Nepal, Sri Lanka	Kuwait	–
21	<i>Ulex europaeus</i>	China, Japan	–	India, Sri Lanka	Turkey	Tajikistan

author also listed 5 species (e.g., *P. crassipes*, *S. molesta*) as important IAPS in aquatic habitats and 20 species (e.g., *C. odorata*, *L. camara*, *M. micrantha*) in terrestrial habitats. More recently, Setyawati et al. (2015) listed 362 plant species from 73 families as invasive in Indonesia. According to Nghiem et al. (2013), there are 20 IAPS in Malaysia, followed by Myanmar (13) and Laos (9). A recent report mentioned more than 20 IAPS (e.g., *C. odorata*, *M. micrantha*, *M. pigra*) in Myanmar (NBSAP Myanmar 2015). Bakar (2004) reported more than 100 weed species in Malaysian agro-ecosystems, many of which have been introduced including *Alternanthera philoxeroides*, *Clidemia hirta*, and *Myriophyllum aquaticum*. A floristic study of floodplain secondary forests in Peninsular Malaysia revealed that the naturalized species contributed 23% (23 of 99 species) to the total species documented (Hashim et al. 2010).

According to Sinohin and Cuaterno (2003), more than 475 plant species were intentionally introduced to the Philippines during historical times, mainly from the Malayan region. Nghiem et al. (2013) reported the presence of 34 IAPS in the Philippines with 10 terrestrial (e.g., *Gmelina arborea* and *L. camara*) and 2 wetland species (*P. crassipes* and *S. molesta*) considered to be highly problematic (Sinohin and Cuaterno 2003). In

Singapore, Corlett (1988) reported the naturalization of 136 plant species, with Fabaceae (29 species) being the most speciose family followed by Asteraceae (15) and Poaceae (13). Among them, 26 species were reported as IAPS including 3 species such as *Cecropia pachystachya*, *L. leucocephala*, and *Spathodea campanulata* (Nghiem et al. 2013). There were 24 and 16 IAPS reported from Thailand and Vietnam, respectively (Nghiem et al. 2013). However, Tan et al. (2012), during a survey of 9 national parks and 1 natural conservation area in Vietnam reported 134 naturalized plant species including 25 IAPS. The National Biodiversity Strategy and Action Plan of Timor-Leste (NBSAP Timor-Leste 2015) reported the presence of at least nine IAPS including *C. odorata* and *L. leucocephala*.

5.2.3 South Asia

In South Asia, one of the most populous regions in the world, research documenting the diversity of IAPS is still insufficient (Pallewatta et al. 2003) and mostly based on reviews of the floristic literature (Khuroo et al. 2011a). In India, the largest country in the region, a number of studies have documented the diversity of alien and/or invasive flora. Khuroo et al. (2012a) compiled a

comprehensive inventory of the alien flora of India, which included 225 invasive species. The families contributing the most IAPS included the Asteraceae (43 species), followed by Amaranthaceae and Euphorbiaceae (14 each) and Poaceae and Solanaceae (13 each). Inderjit et al. (2018) recently reported 471 naturalized plant species in India. Major IAPS in India included *Lantana camara*, *Mikania micrantha*, *Prosopis juliflora*, *Parthenium hysterophorus*, *Ageratina adenophora*, *Pontederia crassipes*, *Salvinia molesta*, *Nymphaea mexicana*, *Alternanthera philoxeroides*, and *Myriophyllum aquaticum*. In Pakistan, Qureshi et al. (2014) documented 73 IAPS including *P. hysterophorus*, *P. juliflora*, *L. camara*, and *Broussonetia papyrifera* which are considered to be highly problematic invasive species. Bambaradeniya (2002) listed 39 IAPS in Sri Lanka including *P. crassipes*, *P. juliflora*, *Mimosa diplotricha*, and *Leucaena leucocephala*. Wijesundara (2010) reported 28 IAPS as being common and widespread. In Nepal, there are 179 naturalized flowering plants, of which 26 are considered invasive (Shrestha 2019). Some of the highly problematic species in Nepal are *A. adenophora*, *Ageratum houstonianum*, *Chromolaena odorata*, *P. crassipes*, *L. camara*, *M. micrantha*, and *P. hysterophorus*. In Bhutan, of 964 alien plant species present, 335 species occur outside cultivated areas of which 131 are casual aliens, 103 naturalized, and 101 invasive (Dorjee et al. 2020). Among the invasive species, major ones are *M. micrantha*, *C. odorata*, *A. adenophora*, *P. hysterophorus*, and *Tithonia diversifolia* (Yangzom et al. 2018). According to the GRIIS database, the number of species naturalized in Bangladesh, Maldives, and Afghanistan are 107, 203, and 56, respectively (Table 5.1). The low number of species recorded in Afghanistan may be because of inadequate research. Bangladesh does not have a comprehensive national list of IAPS, but the National Biodiversity Strategy and Action Plan (NBSAP Bangladesh 2015) reported the occurrence of 15 IAPS including *P. crassipes*, *L. camara*, and *P. hysterophorus*. Biswas et al. (2007) reported five IAPS from Sundarbans, which is a mangrove in Bangladesh. Sujanapal

and Sankaran (2016) mentioned nine IAPS (e.g., *P. crassipes*, *L. camara*, *L. leucocephala*, *Sphagneticola trilobata*) in the Maldives.

5.2.4 West Asia (Middle East)

West Asia includes Turkey, Cyprus, Syria, Lebanon, Israel, Palestine, Jordan, Iraq, Saudi Arabia, Yemen, Oman, the United Arab Emirates, Qatar, Bahrain, Kuwait, and Iran. The region serves as a bridge between the Mediterranean Sea, Black Sea, Caspian Sea, Persian Gulf, Arabian Sea, and Red Sea. According to the available literature, including the GRIIS database, countries with a high number of naturalized plants species in the region include Cyprus (341 species), Turkey (228), Yemen (208), Israel (196), and Iran (118) (Table 5.1). In the region, comprehensive documentation of the alien flora is available only for Turkey, which has 31 species in the family Asteraceae, followed by Poaceae (22), Amaranthaceae (18), and Solanaceae (15) (Uludag et al. 2017). In Cyprus, 22 naturalized plant species are invasive including *Acacia saligna*, *Robinia pseudoacacia*, and *Ailanthus altissima* (Hadjikyriakou and Hadjisterkotis 2002; Spitale and Papatheodoulou 2019). Similarly, there are 13 IAPS (e.g., *A. altissima*, *Azolla filiculoides*, *Pontederia crassipes*) in Turkey (Arslan et al. 2015) and 50 (e.g., *A. altissima*, *P. crassipes*, *Lantana camara*, *Salvinia molesta*) in Israel (Dufour-Dror 2012). In Iran, *A. filiculoides*, *Prosopis juliflora*, *P. crassipes*, *Atriplex canescens*, *Pinus eldarica*, and *R. pseudoacacia* are among the most serious IAPS (A. Naqinezhad, pers.obs.). According to Soorae et al. (2015), there are only 8 IAPS in the United Arab Emirates including *P. juliflora*, *Opuntia ficus-indica*, and *Pennisetum setaceum*. Species such as *Argemone ochroleuca*, *Nicotiana glauca*, *Opuntia stricta*, *O. ficus-indica*, *P. juliflora*, and *Trianthema portulacastrum* have been reported as invasive in Saudi Arabia (Thomas et al. 2016). Alhammadi (2010) lists 12 IAPS for Yemen, including *P. juliflora*, *O. stricta*, *O. ficus-indica*, *P. hysterophorus*, and *Verbesina encelioides*. On

Socotra Island (Yemen), 22 naturalized species have been reported, of which 4 (*Argemone mexicana*, *Calotropis procera*, *Leucaena leucocephala*, and *Parkinsonia aculeata*) are reported to be invasive (Senan et al. 2012) although the current status of some of those listed is being reviewed. *Opuntia stricta* has also been reported as being invasive on Socotra (Coles 2018), but efforts are currently underway to eradicate this species (A.B.R. Witt, pers. obs.).

5.2.5 Central Asia

Central Asia includes five nations (Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan) which are the Republics of the former Soviet Union. This region is located between the Caspian Sea in the west to China in the east, Russia in the north to Iran, and Afghanistan in the south. Little is known about IAPS in this region. According to the GRIIS database, the highest number of naturalized plant species (15) in Central Asia is found in Kazakhstan, which occupies nearly 68% of the land area in the region (Table 5.1). In Kyrgyzstan, there are 14 species of alien plants (Sennikov et al. 2011; Lazkov and Sennikov 2014; Lazkov et al. 2014; Lazkov and Sennikov 2017), though the GRIIS database only lists 5 species as naturalized. Similarly, Tajikistan, the smallest country in the region, has nine alien plant species (Nobis and Nowak 2011a, b; Nobis et al. 2011). We did not find any published scientific study on alien flora of the remaining two countries Turkmenistan and Uzbekistan except for the GRIIS database (Table 5.1).

5.2.6 North Asia

North Asia primarily includes the Asian part of Russia (Siberia and Far East), but for convenience, we have also included the European part of Russia. Vinogradova et al. (2018) list 354 IAPS in Russia, together with their biogeographic and ecological characteristics. Of these, 277 species are present in the European part of Russia,

70 in Siberia, and 79 in the Far East. A higher number of IAPS in the European part of Russia was mainly attributed to higher human population densities associated with high levels of urbanization and associated disturbance to natural ecosystems compared to other regions of Russia (Vinogradova et al. 2018). The most widespread IAPS in Russia include *Acer negundo*, *Echinocystis lobata*, *Erigeron canadensis*, and *Elodea canadensis* (Vinogradova et al. 2018). The GRIIS database shows that 956 alien species are naturalized in Russia (Table 5.1).

In addition to national lists, inventories of alien flora are also available for different regions within Russia. For example, in the Upper Volga region (European part), there are 770 alien plant species with 135 (17.5%) and 32 (4.2%) species naturalized and invasive, respectively (Borisova 2011). Among the IAPS, *A. negundo*, *Bidens frondosa*, and *Impatiens glandulifera* are widespread in the Upper Volga region. In the Moksha River basin within the Volga Upland, there are 314 alien vascular plants which account for 25% of the total flora of this region; among these 46 species are considered to be invasive (Silaeva and Ageeva 2016). In the Middle Volga region, there are 490 alien plant species, of which 59 are invasive or potentially invasive (Senator et al. 2017). In the Middle Urals, 328 species of alien plant species have been reported (Tretyakova 2011). Similarly, in Far East Russia, 292 alien plant species have been reported from the Magadan region (Lysenko 2011), 155 species from the Yakutia region (Nikolin 2014), and 392 species from the Khabarovsk region (Antonova 2013).

5.3 Distribution

Information on the distribution of IAPS is essential for improving our understanding of the processes which drive plant invasion and to develop effective management strategies. In this section, we review spatial distribution of selected IAPS in Asia and discuss natural (e.g., climate and elevation) and anthropogenic factors (e.g., demography and economic growth) that govern diversity

and distribution of IAPS. At the end of this section, we also review the status of plant invasions in protected areas and inland aquatic and wetland ecosystems.

5.3.1 Spatial Distribution

Mapping of spatial distribution of IAPS is an important approach to rapidly assess the extent of invasions across ecosystems and track dispersal vectors and pathways. Geo-referenced distribution data have increasingly been used for the prediction of suitable habitats of IAPS as a part of risk assessment. In Asia, geographic distribution patterns of individual IAPS have been analyzed only for a few species (e.g., *Lantana camara*, *Ageratina adenophora*, *Parthenium hysterophorus*), in a limited number of countries in East, Southeast, South, and West Asia. These analyses, based on climate suitability alone, reveal that the full geographic range of these species has yet to be reached, suggesting that they are likely to increase their distribution. In this section, in addition to distribution mapping of individual species, we also review multispecies studies and highlight the distribution patterns of some of the world's worst species invading different regions of Asia.

Studies Involving Single Species

Among several IAPS in Asia, most distributional studies have been undertaken for *Lantana camara*, *Ageratina adenophora*, and *Parthenium hysterophorus*. Distribution patterns and availability of the suitable habitats for *L. camara* have mainly been undertaken in India (Kannan et al. 2013; Mungi et al. 2020) and also globally (Taylor et al. 2012; Qin et al. 2016). Kannan et al. (2013) reconstructed *L. camara* introductions in India and demonstrated that the widespread occurrence of this species in India was due to its introduction between 1800 and 1900 at different cantonments during British rule. Currently the species is found throughout India with an estimated 39% of forest area invaded (Mungi et al. 2020). The success of *L. camara* in India and

elsewhere has largely been attributed to extensive deforestation leading to the creation of suitable habitats (Mungi et al. 2020). Ecoclimatic models revealed that much of Asia, which is currently uninvaded by *L. camara*, has a suitable climatic condition, and as such this species is likely to expand its distribution into tropical and subtropical regions (Taylor et al. 2012; Qin et al. 2016), in the absence of effective control measures.

Ageratina adenophora is found in several Asian countries, with most studies on its distribution being undertaken in China (Wang and Wang 2006; Zhu et al. 2007; Sang et al. 2010). In China, it was first reported from Yunnan Province in the 1940s, from where it spread north and east at rates of 7–20 km/year between the 1960s and 1990s (Wang and Wang 2006; Zhu et al. 2007). Based on ecoclimatic models, it is likely to increase its range, particularly in the southern and south-central regions including the southeastern coastlands and Taiwan, where large tracts of land are still free from invasions (Wang and Wang 2006; Zhu et al. 2007).

Similarly, *Parthenium hysterophorus* has invaded East, Southeast, and South Asia, but its distribution is only known for South Asian countries (Dhileepan and Senaratne 2009; Ahmad et al. 2019a; Shrestha et al. 2019a). It has invaded all South Asian countries except Afghanistan. In Nepal, *P. hysterophorus* is widespread in the southern part of the country (Tarai and Siwalik regions), from where it is spreading north, especially along road networks (Shrestha et al. 2019a). An ecoclimatic model revealed that parts of the western Himalaya, virtually the entire northeast, and parts of Peninsular India (particularly the coastal parts of Odisha and Andhra Pradesh, southern part of Karnataka and entire Tamil Nadu) are climatically suitable for *P. hysterophorus* (Ahmad et al. 2019a). Most of Sri Lanka and Bangladesh, southern coastal and northeastern part of India, and southern part of Nepal are also a suitable climatic match (Dhileepan and Senaratne 2009). The model also revealed that in addition to South Asia, where the occurrence of *P. hysterophorus* is currently high, there are regions of high climatic suitability in

eastern China, Southeast Asia, and parts of Japan and Korean Peninsula where this species is either absent or has been recorded only at a few locations (Mainali et al. 2015).

Distribution patterns and the climatic suitability of Asia to invasions by *Mikania micrantha*, *Mesosphaerum suaveolens*, *Prosopis juliflora*, and *Ambrosia confertiflora* have also been undertaken. The Western Ghats of south India, parts of northeast India, eastern parts of Vietnam and Laos, southern China, Taiwan, northern Philippines, and parts of south and west Indonesia are a good ecoclimatic match for *M. micrantha* (Banerjee et al. 2019). Padalia et al. (2014) found that nearly 40% of India, mainly in the central part, parts of the western Himalayan foothills, and tropical areas in the northeast, were a good ecoclimatic match for *M. suaveolens*.

Distribution mapping of *P. juliflora* in West Asia revealed that invasive populations were more frequent in Jordan than in Israel, possibly due to high soil moisture and efficient dispersal by domestic herds in Jordan (Dufour-Dror and Shmida 2017). Repeated mapping of *A. confertiflora* in Israel showed that it was first recorded in 1990 at a few locations with populations exploding in the last 15 years (Yair et al. 2019). By 2015, the species was widespread, particularly in the central and northern part of Israel. Occurrence of this species declined with increasing distance from road and rivers, suggesting that they serve as dispersal corridors and provide suitable microhabitat for the establishment of *A. confertiflora*.

Studies Involving Multiple Species

Efforts have also been made to predict suitable niche areas for multiple species in Southeast (SE) and South Asian countries. In SE Asian countries, about 6 million km² has been predicted to be suitable for one or more of ten IAPS (Truong et al. 2017). Species which are likely to invade large areas in Asia include *Ageratum conyzoides*, *Pontederia crassipes*, *Leucaena leucocephala*, *Lantana camara*, and *Mimosa diplotricha*. Based on ecological niche modeling of 155 species currently naturalized in India, Adhikari et al. (2015) found that 49% of the geographic area of the

country is susceptible to further invasions with moderate to high level of climatic suitability. Coastal regions, northeastern region, and Western Himalaya have regions with high climatic suitability. The regions with high climatic suitability that overlapped with anthropogenic drivers of invasions (e.g., dense settlements, villages, croplands) were designated as “invasion hotspots,” and a large proportion of these hotspots lies in global biodiversity hotspots such as the Himalaya, Indo-Burma, Western Ghats, and Sri Lanka (Adhikari et al. 2015). In Nepal, 40% of the total area, mostly representing Tarai, Siwalik, and Middle Mountain regions, has been predicted to have a suitable climate for one to many of the 24 IAPS studied (Shrestha and Shrestha 2019). Areas predicted to be suitable for the highest number of IAPS (14–20 species), based on studies undertaken, are concentrated in central Nepal. In Sri Lanka, the southern and western parts of the country are ecoclimatically a good match for five to eight IAPS, whereas the northern and eastern parts are either unsuitable for many species included in the analysis or suitable only for 1 to 2 species (Kariyawasam et al. 2019).

Distribution of Globally Worst Species

Of the 37 species of vascular plants listed in 100 of the world’s worst invasive species (Lowe et al. 2000; Luque et al. 2014), 21 are present and alien in Asian countries. Among them, the maximum number of species are present in East Asia (18 species), followed by South Asia (17), Southeast Asia (14), West Asia (8), and Central Asia (1), whereas none of these species have been reported from North Asia (Table 5.2). Global modeling also revealed that the areas at high risk to invasion by species included in the list of 100 worst species are located in East, Southeast, and South Asia (Bellard et al. 2013). Most frequently occurring plant species among them are *Pontederia crassipes* (30 countries; 64% of the total 47 countries in Asia), *Lantana camara* (30; 64%), *Leucaena leucocephala* (29; 62%), *Mikania micrantha* (17; 36%), and *Chromolaena odorata* (16; 34%) (Table 5.2, Fig. 5.1). Countries with the highest number of

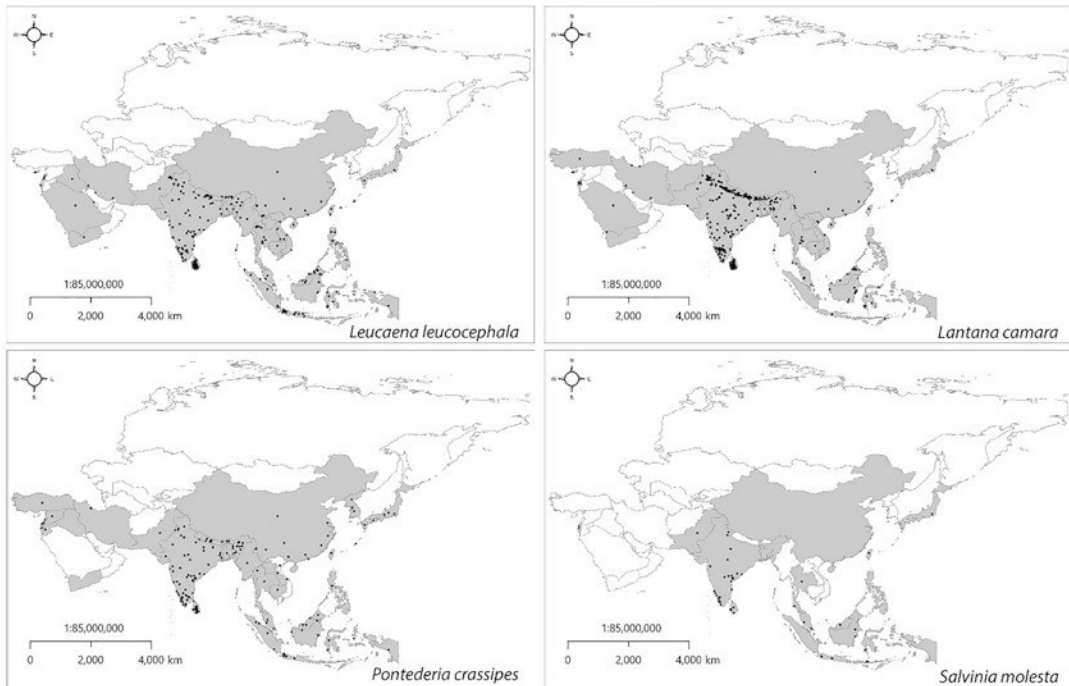


Fig. 5.1 Distribution of most frequently occurring 2 terrestrial (*Leucaena leucocephala* and *Lantana camara*) and 2 freshwater species (*Pontederia crassipes* and *Salvinia molesta*) from the list of the 100 of the world's worst invasive species that are invading Asian countries (shaded). Occurrence data was obtained from GBIF data-

base (www.gbif.org), CABI (2020), other literatures, and individual collections (see Acknowledgment for people contributing personal collections). In few countries, presence of the species was confirmed from the literature, but there was no geographic coordinates available of their precise occurrence locations

these species are India (15 species), China (14), Malaysia (13), and Sri Lanka (12). Countries like Kazakhstan, Kyrgyzstan, Mongolia, Oman, Qatar, Russia, Turkmenistan, the United Arab Emirates, and Uzbekistan have not reported any of these species yet.

5.4 Factors Governing Plant Invasions

Occurrence of IAS is determined by complex interactions between natural (e.g., climate, native biodiversity, species traits) and anthropogenic factors (e.g., propagule pressure, disturbance). Factors that govern diversity and distribution patterns of IAPS have been analyzed in a few countries of Asia. We summarize below how climate, elevation, ecosystem attributes, infrastructure development, demography, and economic growth

govern diversity and distribution of alien plants in Asia. In addition to these factors, residence time (time since introduction) also determines geographic extent of distribution of any species, but this has not been assessed in Asia except in China where it was shown that the number of provinces occupied by an invader increases with time since their introduction (Huang et al. 2010).

5.4.1 Climate and Climate Change

Understanding the role of climate in determining plant distribution is one of the classic topics in ecology (Woodward 1987). However, how climatic variables regulate distribution of alien species is a relatively understudied topic in Asia. A few studies in China suggest that the number of IAPS is high in the warm and moist regions (southeastern China) and declines in the cool and

dry regions (northwest China) (Weber et al. 2008; Wu et al. 2010). In India, tropical states located southward to 20° N have a high number of naturalized plant species with the highest number (332 species) in Tamil Nadu (Inderjit et al. 2018). In the north, the states with higher precipitation during the dry season (e.g., Himachal Pradesh, 232 species) have higher numbers of naturalized species. In general, mean annual temperature and dry season precipitation are the major climate determinants of the number of naturalized plant species in India (Inderjit et al. 2018). A statistical model developed from climate anomalies also revealed a high affinity of studied IAPS to either warmer, drier, or wet places in India (Tripathi et al. 2019). In Nepal, lowland regions with tropical and subtropical climates (i.e., Tarai and Siwalik regions in the south) have higher numbers of IAPS than in the colder highlands (Shrestha 2019).

With climate change it is generally anticipated that the distribution of alien species will also change (Hulme 2017). Climate change makes ecosystems more vulnerable to invasion (Wallingford et al. 2020). It also drives the naturalization rate of introduced species and invasive potential of existing IAPS and sleeper species (Dullinger et al. 2017; Spear et al. 2021). Ecological niche modeling studies in Asia have clearly indicated that the geographic range of the majority of evaluated species will increase in future. For example, climatically suitable regions of all 11 IAPS evaluated are expected to increase, with some species establishing at higher elevations in the Western Himalaya (part of Nepal and India) (Thapa et al. 2018). In another study covering the entire Himalayan range (from Myanmar to Afghanistan), climatically suitable areas for *Ageratina adenophora*, *Chromolaena odorata*, and *Lantana camara* are likely to increase, while those of *Ageratum conyzoides* and *Parthenium hysterophorus* are likely to decrease in the future (Lamsal et al. 2018). Modeling across global ecoregions predicted an increase in plant invasion risks in ecoregions of East Asia (China) and Southeast Asia (Wang et al. 2019). Similarly, climatically suitable areas for *L. camara* may increase in China, but it may shrink in South and

Southeast Asia (Taylor et al. 2012; Qin et al. 2016).

A few studies have also modeled the impacts of climate change on distribution of single or multiple IAPS in China and South Asian countries. Climatically suitable areas will increase in south and southwestern China, particularly in Guangxi, Guizhou, and Yunnan provinces, while there will be some decline in Sichuan Province in the 2080s (Wang et al. 2017). Overall, the suitable area will increase by 16%. There will be a net gain of climatically suitable areas for *L. camara* and *Senna tora* in India (Panda et al. 2018) but a net loss of suitable areas for *C. odorata* and *Tridax procumbens* (Panda and Behera 2019). In a multispecies analysis, Shrestha and Shrestha (2019) showed that the climatically suitable regions will increase for 75% of IAPS in Nepal (16 species, e.g., *L. camara*, *P. hysterophorus*, *Ageratum houstonianum*) and decline for the remaining 25% of IAPS (e.g., *Amaranthus spinosus*, *Bidens pilosa*). In Bhutan, predicted climate change (2041–2060) may increase suitable areas of four IAPS (*A. conyzoides*, *C. odorata*, *L. camara*, and *Mikania micrantha*) but reduce for two species (*A. adenophora* and *P. hysterophorus*) (Thiney et al. 2019). Areas with potential risk of invasion by a higher number of IAPS are likely to increase in Sri Lanka under future climate scenarios (2050 and 2070 for Representative Concentration Pathways, RCP 4.5 and 8.5) (Kariyawasam et al. 2019).

5.4.2 Elevation Gradient

Elevation is an important topographic feature of mountain landscapes which influences climate, such as temperature, precipitation, and solar radiation, and thus the distribution of plants and other organisms. It strongly influences the distribution of IAPS in mountain landscapes by limiting the growth of many species at higher elevations (Alexander et al. 2011). Therefore, a change in diversity of IAPS is expected along elevation gradients. A few studies in Asia have examined this pattern using interpolated, inventory, and plot-level data. While the analyses using interpolated

data from species distribution range have reported unimodal relations (mid-elevation peak), other analyses using inventory and plot-level data have reported a continuous decline in the number of alien species with increasing elevation. For example, using interpolated distribution data, Bhattarai et al. (2014) reported a mid-elevation peak at *ca.* 1100 masl with lower number of naturalized species at lower and higher elevation between 60 m and 4300 masl in Nepal. Using a similar approach, Khuroo et al. (2011b) showed that the species richness of naturalized plants exhibited a unimodal relationship with elevation (500–5000 masl) in Kashmir Himalaya (India), reaching the highest species richness between 1000 and 2000 masl. A similar pattern was also observed in Himachal Pradesh (Western Himalaya, India) with the highest richness of naturalized species at 1000–1100 masl within the elevation gradient of 300–5000 masl (Ahmad et al. 2018).

Using inventory data, Akatova and Akatov (2019) reported that the number of naturalized plant species declined with increasing elevation between 100 and 2400 masl in a mountain range in the Western Caucasus, Russia. Similarly, the number of IAPS declined with increasing elevations (100–4200 masl) in the Arunachal Himalaya (India), with 13, 10, 6, and 1 species occurring in the tropical, subtropical, temperate, and subalpine zones, respectively (Kosaka et al. 2010). In Kashmir Himalaya (India), the number of naturalized species is the highest in valley plains at the lowest elevation, and it declined at higher elevation with only 14 species in the montane alpine zone (Khuroo et al. 2012b).

Using plot-level data, Leung et al. (2009) showed that the number of naturalized plant species declined linearly with increasing elevation (100–1000 masl) in the Tai Mo Shan region of Hong Kong. A similar continuous decline in richness of naturalized plant species has been reported between 1950 and 3500 masl in Eastern Himalaya, China (Yang et al. 2018), between 100 and 1000 masl in temperate mountain forests of northern China (Zhang et al. 2015), and between 1680 and 3750 masl in Kashmir Himalaya, India (Dar et al. 2018).

5.4.3 Ecosystem and Community Features

Ecosystem types and community features largely determine plant invasions at local and landscape levels. Despite the lack of consensus, ecosystems subjected to frequent disturbance that leads to the fluctuation of resources availability are, in general, vulnerable to plant invasions (Davis et al. 2000). Similarly, the diversity of native species exhibits scale-dependent responses to species invading ecosystems (Jeschke et al. 2018). However, these aspects of plant invasions have been little studied in Asia. In China, farmlands are invaded by the highest number of terrestrial IAPS species (162 species out of 170 terrestrial IAPS), followed by forests (29 species) (Xu et al. 2006). In China, regions with a high number of native plant species also tend to have a high number of naturalized species (Wu et al. 2010).

5.4.4 Infrastructure Development, Demography, and Economic Growth

Socioeconomic factors (e.g., per capita domestic growth, population density, proportion of agriculture land) are often bigger drivers of invasions than biogeographic and physical characteristics of the recipient environment (Essl et al. 2019). In regions with high population density and cross-border economic activities, propagule pressure and the proportion of disturbed habitats are high, making such regions highly vulnerable to plant invasions (Davis et al. 2000; Simberloff 2009). One of the best examples that illustrates the roles of economic growth, international trade, and population density on plant invasions is the difference between the number of alien species introduced, both intentionally and accidentally, into South Korea (256) compared to 33 into North Korea, after the division of the Korean Peninsula in 1950 (Kim and Kil 2016). According to Kim and Kil (2016), this disparity could be explained by the fact that South Korea has double the human population of North Korea and gross

national per capita income which is 40 times higher and imports significantly more goods and services than its northern neighbor. In China, the number of IAPS increases with increasing road density (road length per unit area) (Weber and Li 2008). Shanghai (China) witnessed around a sixfold increase in volume of trade between 1980 and 2005, and in the same period, the number of alien species intercepted during border inspections increased more than tenfold (Ding et al. 2008). In India, demographic features such as population density and the percentage of population that live in urban areas are the major determinants of the number of naturalized plant species (Inderjit et al. 2018). In Nepal, richness of naturalized plants species is high in regions with high population density and the number of visiting tourists (Bhattarai et al. 2014).

At sub-national and local levels, transport infrastructure appears to be a major determinant for the occurrence of naturalized and invasive species. In the Kashmir valley (India), alien plant species constitute more than two-thirds of roadside flora (69%), and the richness of naturalized species declines linearly with increasing distance from the road (Dar et al. 2015). In Uttar Pradesh (India), the number of naturalized plant species increase with intensity of road use (low, medium, and high), and for all road use intensity, the species richness and relative importance of naturalized species decline as one moves away from road verges (Sharma and Raghubanshi 2009). In Manas National Park in northeast India, the occurrence of two major IAPS (*Mikania micrantha* and *Chromolaena odorata*) mainly depends on proximity to roads, among other factors (Nath et al. 2019). Similarly, distances from the nearest settlement and roads are the most important factors after tree canopy and distance from rivers in determining the occurrence of IAPS in Bardia National Park of Nepal (Bhatta et al. 2020). In general, roads facilitate plant invasions by serving as dispersal corridors for plant propagules and providing suitable microhabitats (Christen and Matlack 2006).

5.5 Plant Invasions in Special Habitats

5.5.1 Protected Areas

Plant invasions in protected areas (PAs) are increasing worldwide, and cases of successful management are very limited (Foxcroft et al. 2017; Shackleton et al. 2020), suggesting that there will be continued threats from plant invasions to global conservation goals. Despite large geographic coverage and numerous PAs in Asia, the number of studies dealing with plant invasions is very low (Hulme et al. 2014). Limited studies, however, suggest that the PAs of this region (particularly China, Southeast and South Asia, and West Asia) are invaded by a range of IAPS including species such as *Chromolaena odorata*, *Pontederia crassipes*, *Lantana camara*, and *Mikania micrantha*.

There are more than 2500 PAs in China, but studies on biological invasions have only been undertaken in 24 of these (Guo et al. 2017). The number of naturalized species reported in each PA ranged from 3 to 51, with the largest number of species in Dinghushan National Nature Reserve (51) followed by Taohongling (49) and Tianmushan (46). Some of the frequently reported species are *Alternanthera philoxeroides*, *Amaranthus spinosus*, *Euphorbia hirta*, *Erigeron annuus*, *Bidens pilosa*, *C. odorata*, and *Ipomoea purpurea* (Guo et al. 2017). In Laojun Mountain National Park (Yunnan, China), there are 61 naturalized species, of which *Galinsoga quadriradiata*, *Oxalis corniculata*, and *B. pilosa* are the most frequently occurring species (Yang et al. 2018).

In Southeast Asia, knowledge of plant invasions is limited to some PAs in Vietnam, Cambodia, and Indonesia. In a study of 10 PAs in Vietnam, Tan et al. (2012) found 8 to 15 IAPS in each PA with *C. odorata*, *P. crassipes*, *Mimosa diplotricha*, *M. pigra*, *Panicum repens*, and *M. micrantha* reported as the most problematic species. In Cambodia, Renner et al. (2011) reported seven IAPS from six PAs (Central Cardamoms

Protected Forest, Kirirom National Park, Bokor National Park, Seima Biodiversity Conservation Area, Phnom Prich Wildlife Sanctuary, and Mondulkiri Protected Forest) with one to six species in each PA. *Chromolaena odorata* was the most prevalent IAPS and found in all six PAs, even present in core areas in some cases. The Wildlife Conservation Society (2006) found 50 naturalized species, of which 15 were plants, in the Tonle Sap Biosphere Reserve (TSBR) in Cambodia. The most abundant of these were *M. pigra* and *P. crassipes*. In a study covering 8 National Park's (NPs) in the Java region of Indonesia, Padmanaba et al. (2017) reported 67 IAPS (number in each NP ranging from 8 to 27 species), of which 33 occurred only in one NP and *C. odorata* and *L. camara* in all of them. *Ageratina riparia* and *L. camara* were among the most abundant species. A survey of 15 of Indonesia's NPs revealed that they were invaded by 51 plant species, of which *C. odorata* and *L. camara* were among the most problematic species (Setyawati et al. 2012).

In South Asia, information on plant invasions in PAs is available for Nepal, India, and Sri Lanka. Research on plant invasions in India and other South Asian countries is inadequate, possibly because of the traditional focus on wildlife by PA management agencies (Hiremath and Sundaram 2013). In Nepal, PAs located in the southern lowland (Tarai and Siwalik regions) have high number of IAPS (e.g., 18 and 12 species in Chitwan and Parsa National Park, respectively) compared to the PAs in mountain regions (e.g., 5 and 7 species in Langtang National Park and Manaslu Conservation Area, respectively) (Shrestha 2019). Major IAPS in lowland PAs are *L. camara*, *C. odorata*, and *M. micrantha*, while *Ageratina adenophora* is the major IAPS in mountain regions. Chitwan National Park, a major habitat of the one-horn rhino (*Rhinoceros unicornis*) in Nepal, has been severely invaded by *M. micrantha*, among others (Murphy et al. 2013), while the Bardia National Park, a major habitat of tiger, by *L. camara* (Bhatta et al. 2020). In PAs of India, 19 major IAPS have been reported, including *L. camara*, *Prosopis*

juliflora, *C. odorata*, *M. micrantha*, *M. diplotricha*, and *Parthenium hysterophorus* (Hiremath and Sundaram 2013). In Manas National Park, India, *C. odorata* and *M. micrantha* are the most problematic IAPS (Nath et al. 2019). In Sri Lanka, PAs are a good climatic match for a range of species among 14 IAPS studied, including *Panicum maximum*, *L. camara*, *Leucaena leucocephala*, and *Opuntia stricta* (Kariyawasam et al. 2020). In the Himalaya (that includes parts of East, Southeast, and South Asia), 69% (338) of 493 PAs are ecoclimatically a good match for 1 or more of the 5 studied IAPS (*A. adenophora*, *Ageratum conyzoides*, *C. odorata*, *L. camara*, and *P. hysterophorus*) (Lamsal et al. 2018).

5.5.2 Inland Aquatic and Wetland Ecosystems

Inland aquatic and wetland ecosystems have disproportionately high conservation values and provide precious ecosystem services. Biological invasions are considered to be one of the main drivers of ecosystem degradation in these systems (Zedler and Kercher 2004). That said, plant invasions in aquatic and wetland ecosystems of Asia have been poorly studied. In China, Zhan et al. (2017) reported 55 naturalized plant species including algae in these ecosystems, of which 6 are invasive – *Pistia stratiotes*, *Pontederia crassipes*, *Cabomba caroliniana*, *Alternanthera philoxeroides*, *Spartina alterniflora*, and *S. anglica*. Another study, which appears to be more comprehensive, reported 152 aquatic naturalized plant species in China (Wang et al. 2016). In Japan, aquatic and wetland ecosystems are colonized by more than 40 naturalized species; many of them are highly invasive and include *P. crassipes*, *Elodea nuttallii*, *Egeria densa*, *P. stratiotes*, *Myriophyllum aquaticum*, *Gymnocoronis spilanthoides*, *A. philoxeroides*, and *Hydrocotyle ranunculoides* (Kadono 2004). In the Lower Mekong Basin (Cambodia, Lao PDR, Thailand, and Vietnam) of Southeast Asia, important wetland IAPS are *Brachiaria mutica*, *P. crassipes*, *P. stratiotes*, and *M. pigra* (Miththapala 2007).

Pontederia crassipes, *Salvinia molesta*, and *Mimosa pigra* are invasive in almost every country in Southeast Asia (Witt 2017).

In South Asia, freshwater aquatic and wetland ecosystems of India are invaded by several IAPS, of which highly invasive ones are *P. crassipes*, *S. molesta*, and *P. stratiotes* (Shah and Reshi 2012). In Kashmir Himalaya (India) alone, Shah and Reshi (2014) reported 28 species as invasive in wetlands. Wular Lake, the biggest lake in Kashmir Himalaya, is invaded by *Azolla filiculoides* and *Alternanthera philoxeroides* (Keller et al. 2018). Similarly, six IAPS in Nepal are exclusively found in wetlands including some Ramsar sites and include *P. crassipes*, *A. philoxeroides*, *P. stratiotes*, and the semi-aquatic *Ipomoea carnea*, all of which are highly problematic, while *Leersia hexandra* and *Myriophyllum aquaticum* have localized distributions (Shrestha 2019). Species such as *A. philoxeroides*, *P. crassipes*, and *P. stratiotes* are present in wetlands in the Maldives (Sujanapal and Sankaran 2016). In Israel, freshwater wetlands are heavily invaded by *P. stratiotes*, *P. crassipes*, *M. aquaticum*, *A. filiculoides*, and *S. molesta* (Dofour-Dror 2012). *Azolla filiculoides* has also invaded Ramsar sites such as Anzali wetland in northern Iran (Hashemloian and Azimi 2009). Invasions of *P. crassipes* and *P. stratiotes* have also been recently reported from Iranian wetlands (Mozaffarian and Yaghoubi 2015; Bidarlord et al. 2019).

5.6 Native Range and Introduction Pathways

Knowledge of the biogeographic origin of alien species and their introduction pathways are essential for risk assessments, screening at international ports, and Early Detection and Rapid Response (EDRR) against potential invasive species. However, these issues have been poorly studied in Asia.

5.6.1 Native Range

Biogeographic origin of species largely determines invasiveness and spatial extent of distribution in the introduced range. For instance, a

species native to the tropics of South America is more likely to be invasive and widespread in India than species native to more temperate Europe (Khuroo et al. 2012a). Biogeographic origin of alien species has been a subject of analysis only in a few countries as summarized in Table 5.3. Most of the IAPS in Asia originate from tropical America, followed by Africa, Europe, and Oceania. There are obvious gaps in the data presented in Table 5.3 due to lack of adequate information from Central and North Asia. Inclusion of Russia and Central Asian countries may change the scenario. As expected, 31% of 328 alien plants found in the Middle Urals of Russia are native of Asia (outside Russia), followed by species from the Mediterranean region (22%), Europe (outside Russia, 19%), America (mostly temperate North America, 17%), Siberian region (7%), and other regions including Africa (4%) (Tretyakova 2011). Similarly, in North Korea, most (61%) of the alien species are native to other regions in Asia, followed by Europe (37%) and North America (2%) (Son et al. 2009).

Current patterns of geographic origin of alien species in Asia are most likely a result of climatic similarities and propagule pressure due to trade relations. For example, Jiang et al. (2011) attributed the highest contribution of American native plant species to alien flora of China to broad climatic similarity and high volumes of trade between China and North America. Similarly, high contributions of species from China to the alien flora of North Korea can also be attributed to high dependency of North Korea on China for the supply of essential goods (Son et al. 2009). In addition, a few species that are native of tropical America were introduced first to Europe as ornamental plants and subsequently to Asia during European colonization as exemplified by the introduction of *Lantana camara* to India (Kannan et al. 2013).

5.6.2 Introduction Pathways

Managing pathways is one of the major goals of Aichi Target 9 of the Convention on Biological Diversity aimed to combat biological invasions (IUCN-ISSG 2016). Alien species may be intro-

Table 5.3 Geographic contribution to the alien flora of selected countries in Asia

Country/region	#Species included	Native range (% of total)							References
		Americas	Asia	Africa	Europe	Oceania	Unknown/others		
China	861	52	12.7	8.6	13.9	1.6	11.2	Jiang et al. (2011)	
Hong Kong (China)	144	54.2	10.4 ^a	15.3	18.0 ^b	–	2.1	Corlett (1992)	
Indonesia	1936 ^d	40	26	13	9	–	12	Tjitrosoedirdjo (2005)	
Singapore	136	63.2	20.6	9.5	0.7	0.7	5.1	Corlett (1988)	
India	1599 ^d	39	21	20	11	8	1	Khuroo et al. (2012a)	
Nepal	166	74.1	4.2	4.8	8.4	–	8.4	Bhattarai et al. (2014)	
Turkey	340 ^d	44.7	27.6	9.1	7.9 ^c	3.8	6.9	Uludag et al. (2017)	
Mean (± SD)		52.5 ± 12.8	17.5 ± 8.6	11.5 ± 5.0	9.8 ± 5.4	3.5 ± 3.3	6.7 ± 4.2		

^aTropical and subtropical Asia^bAlso includes northern Asia^cAlso include Mediterranean region^dIncludes naturalized and casual/cultivated species

duced by one or more of the following pathways: release, escape, contaminant, stowaway, corridor, and unaided (Hulme et al. 2008). For plants, the most common dispersal pathways worldwide are “escape” (initial intentional introduction but subsequent unintentional escape) and “release” (intentional introduction for release) (Saul et al. 2017). In Asia, most of the species, for which information is available, were introduced through “escape,” “release,” or “contaminant.” Shipping, aquaculture, and aquarium, water gardening, and ornamental trades are the major pathways of the introduction of alien species to aquatic and wetland ecosystems in China and Japan (Kadono 2004; Wang et al. 2016; Zhan et al. 2017). In Turkey, 72% of the alien flora were introduced intentionally (Uludag et al. 2017).

A large number of alien plant species introduced for ornamental purposes have escaped and naturalized in the wild, with several of them becoming serious invasive species. *Lantana camara* is probably the best and most documented example of a garden escape that has devastating environmental and socioeconomic impacts, particularly in South and Southeast Asia. The species was introduced to at least six locations in British cantonments and botanical gardens of British India, of which the first introduction occurred during the 1800s (Kannan et al. 2013). By 1874, it was reported as spreading into the wild (Kannan et al. 2013). There are several other examples of garden escapes. *Leucanthemum vulgare* was introduced as an ornamental to India during the British era and is now invasive in Kashmir and Himachal Pradesh (Khuroo et al. 2010). Mehraj et al. (2018) reported 110 cultivation escapes and 58 accidentally introduced alien plant species in Srinagar city, Kashmir (India). At least 14 IAPS, including *L. camara*, *Pontederia crassipes*, *Prosopis juliflora*, and *Clidemia hirta*, escaped from botanical gardens in Sri Lanka where they were first introduced for ornamental and educational purposes (Wijesundara 2010). Some of the species that escaped from gardens in Southeast Asia are *Caesalpinia pulcherrima*, *Thunbergia grandiflora*, *Ipomoea carnea*, *I. cairica*, *Bougainvillea spectabilis*, and *Coccinia indica* (MacKinnon 2002). Slightly more than

one-third (671 species) of the total alien plant species (1936 species) present in Indonesia are ornamentals and were intentionally introduced (Tjitrosoedirdjo 2005). In Singapore, 32 naturalized plant species were initially introduced as ornamental plants and another 19 as crop species originally cultivated for food, medicine, raw materials, forage, or cover (Corlett 1988). *Salvinia molesta*, one of the worst aquatic weeds globally, was introduced to Sri Lanka for research purposes by the Department of Botany, University of Colombo (Bandara 2010). In Upper Volga region of Russia, some of the invasive woody species such as *Acer negundo*, *Fraxinus pennsylvanica*, and *Populus deltoides* were introduced as landscaping plants from 1950 to 1980 (Borisova 2016).

Several of the species introduced for habitat restoration and livestock fodder have also escaped from cultivated areas and become invasive. Several alien tree species including *Taxodium distichum*, *Cryptomeria japonica*, and *Eucalyptus camaldulensis* were introduced to West and Central Asia for the rehabilitation of degraded forests (Mozaffarian 2005; Lee and Kleine 2009); some of them are well known as invasives. *Leucaena leucocephala* was introduced as a fodder species and for nitrogen fixation to all regions except North and Central Asia (Table 5.2) where the species has invaded natural habitats in many countries (Sankaran and Suresh 2013). *Prosopis juliflora* was introduced to Western Asia for agroforestry purposes but is now invading natural habitats (Hegazy and Lovett-Doust 2016). It was also introduced to South and Southeast Asia for fuelwood where it poses a serious threat to natural ecosystems (Sankaran and Suresh 2013). *Azolla filiculoides* was introduced in ca. 1990 to Egypt (Hegazy and Lovett-Doust 2016) and almost at the same time in Iran as a green manure and fodder for livestock, but the plant soon escaped to irrigation canals and wetlands nearby (Hashemloian and Azimi 2009).

A number of species were accidentally introduced as contaminants of crop imports, especially grains and seeds for planting. For example, it is believed that *Parthenium hysterophorus* was accidentally introduced to India during the 1950s

as a contaminant when wheat (*Triticum aestivum*) was imported from Mexico to Pune, Maharashtra, India (Ahmad et al. 2019a). From Maharashtra, *P. hysterophorus* has spread to all Indian states and most other countries in South Asia including Nepal as a contaminant of agricultural produce or in or on transport vehicles (Shrestha et al. 2019a, b). Similarly, *Ambrosia* spp. might have arrived in Israel through grain shipments (Yair et al. 2019). Likewise, *Ludwigia epilobioides*, *Ambrosia psilostachya*, and *Persicaria lapathifolia* are believed to have been introduced to Iranian rice fields as contaminants of rice seeds (A. Naqinezhad, pers. obs.).

5.7 Environmental and Socioeconomic Impacts

As mentioned in the previous sections, hundreds of naturalized plants have invaded a wide range of regions and ecosystems including agroecosystems and PAs. Based on studies done elsewhere, it is highly likely that the impacts of plant invasions on the environment and socio-economy of this region are significant. However, studies investigating and quantifying the impacts of biological invasions are still scarce in Asia compared to other regions (Hulme et al. 2013). This makes it difficult to assess the magnitude of the problem and hence hinders the possibility of anticipated management interventions and proactive policy responses. In this section, we have highlighted major environmental and socioeconomic impacts of plant invasions with representative examples.

5.7.1 Environmental Impacts

Biodiversity and Ecosystems

Plant invasions have caused serious negative impacts on native ecosystems, including biodiversity and ecosystem services, alteration of biogeochemical cycles, and threats to environmental safety in Asia. Change in species composition and subsequent reduction in species richness and diversity after invasion have been reported for *Ageratina adenophora*, *Carpobrotus edulis*,

Centaurea iberica, *Chromolaena odorata*, *Pontederia crassipes*, *Lantana camara*, *Leucanthemum vulgare*, *Mesosphaerum suaveolens*, *Parthenium hysterophorus*, *Solidago canadensis*, *Spartina alterniflora*, and *Xanthium strumarium*. Fu et al. (2018) reported that *A. adenophora* reduced species richness of understory vegetation by 68% in *Pinus yunnanensis* forest in Yunnan, China, and displaced many native species, particularly those species having low leaf nitrogen content. Similarly, *C. edulis* in coastal habitats of Israel is displacing the coastal iris, *Iris atropurpurea*, a rare species endemic to Israel (Dufour-Dror 2012). In the mountain grasslands of Kashmir Himalaya, *C. iberica* has altered species assemblages, reduced the number and abundance of palatable native species, and reduced species diversity (Reshi et al. 2008). Native plant species richness was 1.25 times higher in non-invaded plots (1 m²) than in plots invaded by *C. odorata* in Nepal (Thapa et al. 2016). Vigorous growth of *P. crassipes* outcompeted native hydrophytes, reducing species richness from 16 to 3 in parts of Dianchi Lake of Yunnan Province in China (Wu 1993). In West Asia, *P. crassipes* has replaced many native aquatic plants in wetlands and aquatic channels (Mozaffarian and Yaghoubi 2015; Hegazy and Lovett-Doust 2016).

Invasion by *L. camara* reduced species richness and diversity by 41% and 16%, respectively, in Siwalik Hills of Himachal Pradesh, India (Singh et al. 2014). In Nepal's Bardia National Park, *L. camara* reduced native plant species richness by more than 50% (Bhatta et al. 2020). Plots invaded by *L. vulgare* had, on average, 4.3–6.7 fewer species than non-invaded plots in Kashmir, India (Ahmad et al. 2019b). Species diversity of non-invaded plots was 3.4 times higher compared to plots invaded by *L. vulgare* (Khuroo et al. 2010). The number of species declined by 46–52% in areas heavily invaded by *M. suaveolens* in Chandigarh, India (Sharma et al. 2017). Locally useful species such as *Justicia adhatoda*, *Dioscorea deltoidea*, and *Murraya koenigii* were completely displaced by *M. suaveolens*. There was a 60–70% reduction in abundance and 35–60% reduction in the number of native species due to invasion by *P. hysteroph-*

orus in Chandigarh, India (Kaur et al. 2019). *Solidago canadensis* has partially displaced more than 30 native species which accounted for 10% of total local native species in Shanghai alone (Lei et al. 2010). Non-invaded plots had 1.3 and 1.7 times higher species richness and diversity, respectively, than plots invaded by *X. strumarium* in the Pothwar region of Pakistan (Qureshi et al. 2019).

In forests, plant invasions inhibit tree regeneration. For example, *Leucaena leucocephala* had detrimental impacts on seed germination and seedling establishment of native tree species on the subtropical oceanic island of Chichijima, Japan (Hata et al. 2007). Similarly, seedling density of *Shorea robusta*, the most important timber species in Nepal, was 2.6 times higher in non-invaded plots than in plots invaded by *C. odorata* (Thapa et al. 2016).

In addition to changes in species composition and diversity, plant invasions also have impacts on a range of other ecological processes. For example, *S. alterniflora* has converted mudflats to meadows and degraded native wetland ecosystems in the Yangtze River estuary (Li et al. 2009; Liu et al. 2012). Though there is no empirical evidence, it is believed that invasive species like *L. camara* alter fire regimes, particularly in regions with a dry climate, contributing to the loss of forests (Hiremath and Sundaram 2005).

Impacts on Animals

Only a few studies have examined the impacts of plant invasion on animals in Asia. *Spartina alterniflora* has resulted in loss of shorebirds' foraging habitats and change in community structure and diets of native arthropods in the Yangtze River estuary, China (Li et al. 2009; Liu et al. 2012). During extensive field studies, one of the authors (A.B.R. Witt) observed some impacts of IAPS on flagship wildlife species in Southeast Asia: the Sumatran rhino, Sumatran elephant, and Sumatran tiger in the Bukit Barisan Selatan National Park (and other protected areas in Sumatra island) that are greatly affected by the dense smothering habit of *Merremia peltata* and the near extinction of the rare banteng (*Bos javanicus*) in Baluran National Park due to over

70% loss of its primary habitat of grass savanna by *Acacia nilotica* (ABR Witt, pers. obs.). Invasion by *Prosopis juliflora* in Vettangudi Bird Sanctuary of south India has degraded nesting habitat of breeding birds due to the high probability of eggs and chicks falling to the ground from the nests in this plant (Chandrasekaran et al. 2014). In Nepal's Chitwan National Park, a World Natural Heritage Site, *Mikania micrantha* has invaded 44% of the habitat of endangered one-horn rhino with potential negative impacts on forage supply due to smothering of many native species by the weed (Murphy et al. 2013).

Impacts on Soil

Changes in soil chemistry, nutrient content, and availability have been reported due to invasions by *Ageratina adenophora*, *Chromolaena odorata*, *Parthenium hysterophorus*, *Mikania micrantha*, *Mesosphaerum suaveolens*, *Leucanthemum vulgare*, and *Spartina alterniflora*. Soil in *A. adenophora*-invaded sites of southwestern Yunnan Province, China, had 4.32 mg/kg more nitrogen than non-invaded soil (Zhao et al. 2019). The invaded soil also had higher rates of microbial-mediated functional processes such as nitrogen fixation, nitrification, and ammonification than in the non-invaded soil. Invasion by *C. odorata* also significantly increases labile and total carbon and nitrogen fractions in tropical savanna soils (Wei et al. 2017). Organic carbon, nitrogen, phosphorus, and potassium were higher in *P. hysterophorus*-invaded grassland soils than in non-invaded ones in Nepal (Timsina et al. 2011). However, in Chandigarh, India, the concentrations of organic matter, nitrogen, phosphorus, and potassium were lower in the *P. hysterophorus*-invaded soil than in non-invaded sites (Kaur et al. 2019). Invasion by *M. micrantha* increases soil enzyme activities and abundance of aerobic bacteria but reduces the abundance of anaerobic bacteria in comparison to non-invaded sites (Li et al. 2006). *Mikania micrantha* also enhances nutrient cycling during early stages of secondary succession following slash-and-burn agriculture (Swamy and Ramakrishnan 1987). *Mesosphaerum suaveolens* invasions increase

soil organic matter, organic carbon, and electrical conductivity (Sharma et al. 2017). Ahmad et al. (2019c) reported that invasion by *L. vulgare* in Kashmir Himalaya, India, had a significant impact on key soil properties with soil pH, water content, organic carbon, and total nitrogen significantly higher in the invaded plots as compared with the uninvaded plots. In contrast, the electrical conductivity, phosphorous, and micronutrients, viz., iron, copper, manganese, and zinc, were significantly lower in the invaded plots as compared with the uninvaded plots. The results indicated that *L. vulgare*, by altering key properties of the soil system, influences nutrient cycling processes and facilitates positive feedback for itself. In wetland ecosystems of Yangtze River estuary, China, *S. alterniflora* has enhanced storage of carbon dioxide and increased the inorganic nitrogen pool (Li et al. 2009).

5.7.2 Socioeconomic Impacts

Agriculture and Aquaculture

IAPS are reported to have negative impacts on agricultural production. In terms of the threats of biological invasions to the agricultural sector, four of the five countries most threatened by IAPS are located in Asia; they are Mongolia, Nepal, Bangladesh, and Cambodia (Paini et al. 2016). In Nepal, reduced agriculture production, forage supply, and livestock poisoning are the major impacts of IAPS among farming communities (Shrestha et al. 2019b). Local communities ranked *Ageratum houstonianum* as the most problematic weed in their agriculture production system, mainly due to its toxicity to livestock and high labor cost of weeding. *Mikania micrantha* invasion reduces fodder supply and subsequently increases time to collect fodder by local communities from forests in Nepal (Rai and Scarborough 2015). *Pontederia crassipes* blocks waterways, affects water transport for agriculture and tourism, covers lakes and rivers, causes algal blooms, and reduces aquatic production in China (Ding et al. 2001). Invasions by *Azolla filiculoides* and *Alternanthera philoxeroides* in Wular Lake,

Kashmir (India), impact negatively on fishing and the availability of wild edible plants (Keller et al. 2018). In Turkey, 40 of 51 alien plant species have socioeconomic impacts, mainly on agricultural production and human health (Yazlik et al. 2018a). The highest ranking species in terms of socioeconomic impacts are *P. crassipes* and *Lantana camara*. Similarly, *Ipomoea triloba* has substantially increased weeding cost in cotton farms of Turkey (Yazlik et al. 2018b).

Human and Animal Health

Invasive alien plant species also threaten public health and social well-being. In China, *Pontederia crassipes* is reported to provide habitats for mosquitoes and flies, thereby affecting public health (Ding et al. 2001). *Ambrosia artemisiifolia* and *A. trifida* produce copious amount of pollen, compounding health problems like rhinitis, oculorhinitis, asthma, and skin irritations (Li et al. 2015). *Ageratina adenophora* pollen contains aromatic and pungent chemicals causing allergenic reactions in people (Zhu et al. 2007). In Japan, the recurrent bouts of sneezing, nasal congestion, and tearing and itching of the eyes are caused by seasonal allergies to the pollen of certain plants including alien *Ambrosia* species and alien meadow grasses such as *Lolium multiflorum*, *L. perenne*, *L. x hybridum*, and *Dactylis glomerata* (Saito and Ide 1994). In Israel, the allergenic effect of *Ambrosia confertiflora* pollens to humans has been reported (Yair et al. 2019). Respiratory allergy and dermatitis caused by *Parthenium hysterophorus* are the most common type of plant dermatitis in India, which may be life threatening to sensitive individuals (Sharma and Verma 2012). It mainly affects exposed body parts such as the face, neck, hands, and legs. Similar negative health impacts of *P. hysterophorus* to human have been also reported in Nepal (Shrestha et al. 2015).

There are few studies reporting impacts of IAPS to livestock health in Asia. For example, consumption of *A. adenophora* has been reported to cause acute asthma, diarrhea, depilation, and even death of livestock in China (Zhu et al. 2007). *Ageratum houstonianum* is reported to have poi-

soning effects on livestock in Nepal (Shrestha et al. 2019b). Several cases of livestock death due to consumption of *Mimosa diplotricha* have been also observed in southeastern districts of Nepal (BB Shrestha, pers. obs.). Impact of IAPS to wildlife health has not been reported yet.

Economic Costs

Few studies have evaluated the economic costs of invasive alien species in Asian countries. In China, economic losses due to invasive alien species (plants and other organisms) were estimated to be 14.45 billion USD per year in 2000 (which was 1.36% of GDP) (Xu et al. 2006). Of the total losses, the direct losses associated with damage and control costs in agriculture, forestry, aquaculture, transportation, and health accounted for 16.59% and the indirect losses associated with loss of ecosystem services 83.41%. Nghiem et al. (2013) estimated that the total annual cost of all invasive alien species associated with agriculture, human health, and environment in Southeast Asia amounted to 33.2 billion USD but clearly stated that this was likely to be a conservative estimate. Most of these impacts (90%) were associated with the agricultural sector (29.3 billion USD) where information is more readily available. Economic losses in India due to IAPS on crop production and pasture were estimated to be 38.7 USD billion per year (Pimentel et al. 2001).

A few studies have estimated economic cost of individual species. In China, the annual losses in livestock production due to the effect of *Ageratina adenophora* were estimated to be 162 million USD, and the losses in services of grassland ecosystems were 0.4 billion USD (Xu et al. 2006; Ding et al. 2007). On Nei Lingding Island (Guangdong Province, China), the economic loss caused by *Mikania micrantha* was reported to range from 0.56 to 1.6 million USD per year (Zhong et al. 2004). Over 12 million USD per year was spent in China on the manual removal of *P. crassipes* between 1991 and 2001, and 128 million USD was spent in 1996 for manual removal of several weeds in Wenzhou City of China's Zhejiang Province (Ding and Xie 1996; Ding et al. 2001). In India, total cost associated with damage and control of *Parthenium hysterophorus* in agroecosystems

between 1955 and 2009 was estimated to be 2.067 trillion INR (equivalent to 26.8 USD billion as per the exchange rate of 15 April 2020) (Sushilkumar and Varshney 2010). Reduced profitability of teak (*Tectona grandis*) plantations due to invasion by *M. micrantha* has been also reported from Kerala, India (Muraleedharan and Anitha 2000). In Punjab Province of Pakistan, the annual cost of *P. hysterophorus* invasion associated with crop and livestock production, health, and social well-being was estimated to be 913 USD per household (Bajwa et al. 2019).

5.8 Management

A variety of management interventions have been developed and implemented in Asia. The management options for IAPS may vary according to the species in question, stage of invasions, the habitat invaded, land use, farming system, size of invasion, time, socioeconomic condition, and available resources. According to Padmanaba et al. (2017), current management efforts are reactive, localized, and intermittent, with currently available resources being insufficient for early detection and prompt responses in PAs in Java, Indonesia. Unfortunately, a similar scenario is prevalent in most parts of Asia. To improve control measures against IAPS, many comprehensive management approaches are widely adopted and used in China and some other Asian countries, combining different physical, chemical, ecological, and biological control methods (Yang et al. 2017; Clements et al. 2019). Generally, these integrated control methods for IAPS are usually designed to make up for shortcomings of individual control applications and can achieve better environmental protection, economic returns, and control (Clements et al. 2019). Integrated pest management interventions that incorporate ecosystem-based and environment-friendly approaches have been initiated in Central Asia (Maredia and Baributsa 2007). In the following sections, we discuss various management approaches being developed and implemented in Asia, including community participation and policy responses.

5.8.1 Physical Methods

Physical control techniques for IAPS include hand pulling or uprooting, slashing, ringbarking, ploughing, and similar interventions, most of which are widely practiced in Asia by farmers and local communities. However, these approaches are seldom documented in the scientific literature, and their effectiveness has been rarely investigated. Physical control techniques could be effective for small, localized invasions but are largely ineffective for widespread and abundant invasions across the landscape. For example, cutting *Lantana camara* during the wet season for biomass by local communities can significantly reduce its abundance at local level, allowing recolonization by native species (Kannan et al. 2016). Similarly, frequent manual removal of *Mikania micrantha* biomass at a local scale while retaining native vegetation may reduce its competitiveness (Rai et al. 2012). Extra precautions are needed to prevent regeneration and dispersal from plant parts which can easily regenerate from stem fragments (Huang et al. 2015). Physical control is also labor intensive and difficult when the IAPS is thorny (e.g., *Mimosa diplotricha*). Despite some limitations, physical methods can be important components of an integrated management strategy.

In Nepal, local communities remove *Chromolaena odorata*, *Ageratina adenophora*, and *Lantana camara* from forests and use their biomass to produce compost and bio-briquettes (Shrestha 2019; Shrestha et al. 2019a, b). Wetland IAPS such as *Pontederia crassipes*, *Pistia stratiotes*, and *Alternanthera philoxeroides* are being removed manually or by using weed harvesters (Shrestha 2019). Site restoration and follow-up control activities after physical removal of IAPS are essential to sustain efficacy. For example, in Kashmir Himalaya, India, control of aquatic IAPS (e.g., *Azolla filiculoides*, *Nymphaea mexicana*) through manual and mechanical measures in Dal Lake has failed due to lack of follow-up action. However, these programs have benefits beyond biodiversity because of local community support. The mechanical removal of aquatic inva-

sive plants provides livestock fodder to local population, and the manual control programs provide daily wage-based employment opportunities (Khuroo et al. 2009; McDougall et al. 2011).

In Israel, physical control is being practiced in a few nature reserves under the supervision of the Israel Nature and Parks Authority (INPA) (Dufour-Dror 2012). In most cases, it is carried out either by uprooting individual plants, by cutting them down, or, in the case of wetland species, by simply collecting the plants from the water bodies and disposing them. Another method attempted to control *Acacia saligna* in Israel is solarization, which uses transparent plastic sheets to cover the soil surface in order to induce seed germination (Cohen et al. 2008). High temperature maintained beneath the plastic eventually kills the seedlings and reduces the persistent soil seed bank.

5.8.2 Chemical Methods

Herbicides are generally an effective control method for IAPS, especially in regions where herbicides are affordable, due to their relatively high efficacy and better returns on application costs (Clements et al. 2019). A broad selection of herbicides has been evaluated for use on IAPS. These herbicides containing the active ingredients 2,4-dichlorophenoxyacetic acid, glyphosate, sulfometuron methyl, paraquat, glufosinate, and picloram are mostly used for control of IAPS, especially *Ageratina adenophora* and *Mikania micrantha* (Yang et al. 2017; Clements et al. 2019). Various combinations of triclopyr, picloram, glyphosate, and diuron have been found effective in controlling *M. micrantha* in teak plantations in Kerala, India (Sankaran et al. 2017).

In Israel and Cyprus, improved methods of chemical applications such as drill-fill (drilling holes on the lower part of trunks and injecting herbicides), cut-stump (felling trees by chainsaw and application of herbicides on outer rim of the stump), and frilling (removal of bark by knife and application of herbicides) techniques have

been successfully used for control of invasive tree species such as *Acacia saligna*, *Ailanthus altissima*, *Robinia pseudoacacia*, and *Dodonaea viscosa* (Dufour-Dror 2013). While these methods have minimum undesirable chemical impacts to the environment, they are labor intensive and require access to every individual tree to be treated.

5.8.3 Biological Control

Biological control of IAPS is environmentally friendly and sustainable (Seastedt 2015). Despite a large number of IAPS, biological control has only been practiced in a few countries in Asia. The first biological control agent, *Dactylopius ceylonicus* (Hemiptera: Dactylopidae), was accidentally introduced from Brazil to India in 1795 where it successfully controlled *Opuntia monacantha* (Cactaceae) in 5–6 years (Rabindra and Bhumannavar 2009). The intention was to introduce *D. coccus* for dye production, but the wrong cochineal was inadvertently introduced. *Dactylopius ceylonicus* was then introduced to Sri Lanka in 1865 to control *O. monacantha*, the first deliberate international transfer of a biological control agent (Rabindra and Bhumannavar 2009). In 1933, China initiated a biological control program with the introduction of two agents, *Ophiomyia lantanae* and *Lantanophaga pusillidactyla*, into Hong Kong for the control of *Lantana camara* (Shen et al. 2018). Over the period of more than 100 years, several biological control agents have been released in Asia with variable success. A literature review revealed that 36 biological control agents (31 arthropods and 5 fungi) targeted for 17 species (1 pteridophyte and 17 angiosperms) are established in different Asian countries (Table 5.4). According to Day and Witt (2019), 15 countries in Asia have intentionally released 42 biological control agents against 19 weed species. The highest number of biological control agents are present in China (18 species) followed by India (16), Thailand (11), Vietnam (6), Timor-Leste (4), Sri Lanka (4), Myanmar (3), Nepal (3), Indonesia (2), Malaysia (2), the Philippines (2), Pakistan (1), Laos (1), and Israel (1) (Table 5.4).

The largest number of biological control agents (10 species) targeted *Lantana camara*; 3 for each of *Chromolaena odorata*, *Pontederia crassipes*, and *Mimosa pigra*; 2 for each of *Ageratina adenophora*, *Ambrosia artemisiifolia*, and *Parthenium hysterophorus*; and 1 agent each for the remaining 11 species (Table 5.4). Only a subset of these species was deliberately introduced while others have spread from neighboring countries. For example, ten biological control agents targeting seven IAPS from neighboring countries have spread naturally and established in China (Shen et al. 2018). Similarly, three agents have established in Nepal after spreading from other Asian countries (Shrestha 2019). Relatively high damage has been observed on *Salvinia molesta* (in India), *A. artemisiifolia* (China), *Opuntia* spp. (India, Sri Lanka, and Israel), and *Mimosa diplotricha* (Timor-Leste) by their respective biological control agents. Impact of many other agents on the target species is either low or moderate in Asia. While it is essential to understand the factors that determine the effectiveness of established biological control agents through regular monitoring, search for new and effective biological control agents targeting highly problematic IAPS should also be continued. Further promotion of biological control programs by countries in Asia as a major component of the integrated management is imperative for long-term and sustainable control of IAPS.

5.8.4 Ecosystem-Based Approaches

Invasibility of any ecosystem depends on its attributes such as successional stage, disturbance regime, and species composition, among others. Minimization of disturbance and manipulation of species composition in semi-natural ecosystems (e.g. agroforestry system, managed pasture) can improve performance of native communities and competitively suppress IAPS, thereby complementing the traditional methods of physical, chemical, and biological controls. One emerging field of research on ecosystem-based management is the use of native or useful and noninvasive alien species to suppress growth and reproduction of IAPS in managed forests, graz-

Table 5.4 Established biological control agents with their targeted invasive alien plant species in different Asian countries

Targeted species [family]	Biocontrol agents [family]	Countries with established population	General impacts	References
<i>Salvinia molesta</i> [Salviniaceae]	<i>Cyrtobagous salviniae</i> [Curculionidae]	India	High	Rabindra and Bhumannavar (2009)
<i>Alternanthera philoxeroides</i> [Amaranthaceae]	<i>Agasicles hygrophila</i> [Chrysomelidae]	China, Thailand	Moderate	Shen et al. (2018), Day et al. (2018)
<i>Ageratina adenophora</i> [Asteraceae]	<i>Passalora ageratinae</i> [Mycosphaerellaceae]	China	Low	Shen et al. (2018)
	<i>Procecidochares utilis</i> [Tephritidae]	China, Nepal, India, Thailand	Low	Day et al. (2018), Shen et al. (2018), Shrestha (2019)
<i>Ambrosia artemisiifolia</i> [Asteraceae]	<i>Ophraella communa</i> [Chrysomelidae]	China	High	Shen et al. (2018)
	<i>Epiblema strenuana</i> [Tortricidae]	China	Moderate	Shen et al. (2018)
<i>Ambrosia trifida</i> [Asteraceae]	<i>Puccinia xanthii</i> ssp. <i>ambrosiae-trifidae</i> [Pucciniaceae]	China	Variable	Shen et al. (2018)
<i>Chromolaena odorata</i> [Asteraceae]	<i>Acalitus adoratus</i> [Eriophyidae]	China, Lao PDR, Myanmar, Thailand, Vietnam	Slight	Day et al. (2018), Shen et al. (2018)
	<i>Cecidochares connexa</i> [Tephritidae]	India, Indonesia, Philippines, Timor-Leste	Moderate	Rabindra and Bhumannavar (2009), Shen et al. (2018)
	<i>Pareuchaetes pseudoinsulata</i> [Arctiidae]	India	??	Rabindra and Bhumannavar (2009)
<i>Mikania micrantha</i> [Asteraceae]	<i>Puccinia spegazzinii</i> [Pucciniaceae]	Taiwan (China), India	Moderate	Rabindra and Bhumannavar (2009), Shen et al. (2018)
<i>Parthenium hysterophorus</i> [Asteraceae]	<i>Puccinia abrupta</i> var. <i>parthenicola</i> [Pucciniaceae]	China, Nepal	Low	Shen et al. (2018), Shrestha (2019)
	<i>Zygogramma bicolorata</i> [Chrysomelidae]	Nepal, India, Pakistan	Moderate	Shen et al. (2018), Shrestha et al. (2019a)
<i>Xanthium strumarium</i> [Asteraceae]	<i>Puccinia xanthii</i> [Pucciniaceae]	Sri Lanka, Timor-Leste	Moderate	Shen et al. (2018)
<i>Opuntia ficus-indica</i> [Cactaceae]	<i>Dactylopius opuntiae</i> [Dactylopiidae]	Israel	High	Shen et al. (2018)
<i>Opuntia stricta</i> [Cactaceae]	<i>Dactylopius opuntiae</i> [Dactylopiidae]	India, Sri Lanka	High	Shen et al. (2018)
<i>Opuntia elatior</i> [Cactaceae]	<i>Dactylopius opuntiae</i> [Dactylopiidae]	India	High	Rabindra and Bhumannavar (2009)
<i>Opuntia monacantha</i> [Cactaceae]	<i>Dactylopius ceylonicus</i> [Dactylopiidae]	India, Sri Lanka	High	Rabindra and Bhumannavar (2009)
<i>Leucaena leucocephala</i> [Fabaceae]	<i>Acanthoscelides macrophthalmus</i> [Chrysomelidae]	China	Low	Shen et al. (2018)
<i>Mimosa diplotricha</i> [Fabaceae]	<i>Heteropsylla spinulosa</i> [Psyllidae]	Timor-Leste	High	Shen et al. (2018)

(continued)

Table 5.4 (continued)

Targeted species [family]	Biocontrol agents [family]	Countries with established population	General impacts	References
<i>Mimosa pigra</i> [Fabaceae]	<i>Carmentia mimosa</i> [Sesiidae]	Malaysia, Vietnam	Moderate	Shen et al. (2018)
	<i>Acanthoscelides puniceus</i> [Chrysomelidae]	Thailand, Vietnam	Low	Day et al. (2018)
	<i>Acanthoscelides quadridentatus</i> [Chrysomelidae]	Thailand, Vietnam	Low	Day et al. (2018)
<i>Pontederia crassipes</i> [Pontederiaceae]	<i>Neochetina bruchi</i> [Eirrhinidae]	China, Thailand, India	Moderate	Shen et al. (2018), Day et al. (2018);
	<i>Neochetina eichhorniae</i> [Eirrhinidae]	China, Thailand, India	Moderate	Shen et al. (2018), Day et al. (2018)
	<i>Orthogalumna terebrantis</i> [Galumnidae]	India	Low	Rabindra and Bhumannavar (2009)
<i>Lantana camara</i> [Verbenaceae]	<i>Calycomyza lantanae</i> [Agromyzidae]	China, Thailand, Vietnam	Low	Day et al. (2018), Shen et al. (2018)
	<i>Hypenaceratalis</i> [Erebidae]	China	Low	Shen et al. (2018)
	<i>Lantanophaga pusillidactyla</i> [Pterophoridae]	China	Low	Shen et al. (2018)
	<i>Crociosema lantana</i> [Tortricidae]	China	Low	Shen et al. (2018)
	<i>Ophiomyia lantanae</i> [Agromyzidae]	China, India, Myanmar, Thailand, Vietnam	Low	Rabindra and Bhumannavar (2009), Day et al. (2018), Shen et al. (2018)
	<i>Lantanophaga pusillidactyla</i> [Pterophoridae]	China, Myanmar, Thailand	Low	Shen et al. (2018)
	<i>Octotoma scabripennis</i> [Chrysomelidae]	India	Moderate	Rabindra and Bhumannavar (2009), Shen et al. (2018)
	<i>Teleonemia scrupulosa</i> [Tingidae]	India, Indonesia, Malaysia, Philippines, Sri Lanka, Thailand, Timor-Leste	Moderate	Shen et al. (2018)
	<i>Uroplata girardi</i> [Chrysomelidae]	India, Philippines	Moderate	Rabindra and Bhumannavar (2009), Shen et al. (2018)
<i>Epinotia lantana</i> [Tortricidae]	India	Low	Rabindra and Bhumannavar (2009)	

ing grasslands, and agroecosystems. These ecological methods are widely used through plant-plant competition, utilizing parasitic plants, soil fungi competition, and allelopathy (Clements et al. 2019). A number of greenhouse or field experiments were conducted in China to evaluate the competitive capacity of replacement plants against the invasive *Ageratina adenophora*. Many local plants have been demonstrated as

ideal candidates of replacement plants, such as *Trifolium repens*, *T. pratense*, *Pennisetum hydridum*, *Setaria yunnanensis*, *Eupatorium fortunei*, *Chenopodium serotinum*, *Setaria sphacelata*, and *Pennisetum clandestinum* (Yang et al. 2017). Similarly, some plant species such as *Cuscuta campestris*, *Macaranga tanarius*, and *Heteropanax fragrans* can suppress *Mikania micrantha* in China (Clements et al. 2019). Sweet

potato (*Ipomoea batatas*), an important cash and food crop widely grown in the world, is reported to suppress four IAPS, *M. micrantha*, *Ageratum conyzoides*, *Bidens pilosa*, and *Galinsoga parviflora* (Shen et al. 2015, 2019). In a field experiment conducted in northern Pakistan, growth of *Parthenium hysterophorus* was suppressed by >70% when grown together with fodder species such as *Sorghum almum*, *Cenchrus ciliaris*, and *Chloris gayana* (Khan et al. 2014).

Habitat restoration by introducing native species has also been suggested for the control of *Acacia saligna* in sand dunes (El-Bana 2008). Some of the ecosystems inherently resist plant invasions. For example, soil and vegetation of undisturbed, late-successional forests may confer resistance to the establishment of *M. micrantha* (Hou et al. 2011). When density of native species is maintained at a high level, the negative impacts of invasive species such as *A. adenophora* may be weakened (Thapa et al. 2017).

5.8.5 Community Awareness and Public Participation

Community participation is important for the successful implementation of IAS management strategies. It is also essential from the ethical point of view and to meet legal compliance requiring public participation in decision-making, including access of communities to information related to environmental matters (Boudjelas 2009). Efforts have been made to produce community awareness and education materials (e.g., identification kit, booklets) for wider dissemination. For example, the International Centre for Integrated Mountain Development (ICIMOD), an organization working in Hindu Kush Himalaya, produced a community training manual for the management of IAPS in this region (Joshi et al. 2016). Publication of a bilingual (English and Nepali) field guide with descriptions of 27 IAPS found in Nepal has been planned in 2021 (Adhikari et al. 2021). A similar field guide is available for IAPS of Bhutan (Yangzom et al. 2018),

Indonesia (Setyawati et al. 2015), Israel (Dufour-Dror 2012), Southeast Asia (Witt 2017), forests of Asia, and the Pacific Region (Sankaran and Suresh 2013). Attempts in creating awareness of IAPS at subnational level include publication of the *Handbook on Invasive Plants of Kerala*, India, by the Kerala State Biodiversity Board (Sankaran et al. 2013). A number of countries are also implementing participatory IAPS control programs by involving local communities. For example, the people of Ranupani Village of Indonesia, with support from the Bromo Tengger Semeru National Park management, have managed to clear about 65% of *Salvinia molesta* from the surface of the lake (UN Environment 2019). Community-based organizations are involved in the removal of IAPS from wetlands (including Ramsar sites – Pokhara lake cluster and Beeshajari lake system) and community managed forests in Nepal (Shrestha 2019). Parthenium awareness week is an annual event which has been regularly observed in India to motivate communities for the management of *Parthenium hysterophorus*. For example, tens of thousands of people, from school children to politicians, in 19 states of India actively participated during Parthenium Awareness Week-2009 (Varshney and Sushilkumar 2009). We envisage that millions of people and thousands of community-based organizations are involved in the management of IAPS in Asia, but these efforts and activities are yet to be documented and recognized.

Local communities, as “citizen scientists,” are important stakeholders in generating knowledge that can support scientific publications and implement invasive species policy decisions (Groom et al. 2019). However, the citizen science approach is relatively rare in Asia compared to other regions of the world. For example, Johnson et al. (2020) reported 26 citizen science initiatives reporting invasive alien species that had led to publication of 31 scientific papers; these initiatives were mostly from Western Europe (11) and North America (10) and surprisingly none from Asia.

5.8.6 Policy Responses

Asian countries formulate policies, devise programs, form institutions, and invest in research and community awareness to tackle the challenges posed by the IAS. We reviewed national reports of Asian countries submitted to the Convention on Biological Diversity (<https://www.cbd.int>, accessed 15 April 2020) and found a wide range of variations in the policy response to manage IAS (unless stated, please refer country national reports for details). Some countries, like Japan, have separate legislations that is solely focused on IAS, the Invasive Alien Species Act, promulgated in 2005. Similarly, different laws and regulations regarding IAS, such as the Domestic Animals Epidemic Prevention Regulation and Plant Quarantine Regulations, the Quarantine Law on Import and Export of Animals and Plants, the Protection Law for Wildlife, the Law on Hygienic Quarantine, the Living Modified Organisms Act, and so forth, have been issued in East Asia (Xie et al. 2001; Washitani 2004; Son et al. 2009; Yan et al. 2012). South Korea and India have other legislations that deal with IAS. In South Korea, Conservation and Use of Biodiversity Act has a provision which designates potentially high-risk species that may harm the ecosystem if introduced to the country. Under this provision, species are subject to evaluations of their risk to the ecosystem and require approval from the Ministry of Environment when imported or introduced to South Korea.

Asian countries have also formed formal and informal institutions from central to local level dedicated to IAS management. In Malaysia, a high-level National Committee on Invasive Alien Species was established for the management of IAS to implement the National Plan of Action for Prevention, Eradication, Containment, and Control of Invasive Alien Species 2014–2018. Russia also created a National Center for Foreign Species to oversee programs and activities related to IAS management in the Russian Federation territory. Similarly, national plans were also prepared in

the Philippines (National Invasive Species Strategy and Action Plan 2016–2026), Indonesia (National Strategy and Directive Action Plan for Management of Invasive Alien Species), and Malaysia (National Action Plan for the Prevention, Eradication, Containment, and Control of Invasive Alien Species) to serve as a roadmap in preventing the introduction and spread of IAS. In Nepal, a national strategy for the management of IAS is in the process of approval from the Ministry of Forest and Environment (Shrestha 2019). China has formally set up a dedicated institution under the Ministry of Agriculture and henceforth set up an emergency response office to address the invasion of alien species and organized on-site elimination of IAS and emergency responses. In Thailand, a Working Group on Alien Species has been formed under the National Subcommittee on Convention on Biological Diversity. This Working Group provides the operational guidelines that were endorsed by the Cabinet on February 2, 2018, to control and prevent the loss of biodiversity due to IAS. A country scale risk assessment framework for IAS was developed in Malaysia. Plans were not only seen at the central level but also at the local level in some Asian countries. For example, local-level plans were prepared by 17 municipal governments across South Korea to develop and implement their own annual plans in addition to the Ministry of Environment's plans to manage alien species. Local-level plans for controlling specified IAS have also been formulated in Japan.

Despite some exceptions, many Asian countries have prepared databases of IAS. Countries like Qatar, Saudi Arabia, and Maldives have little or almost no information on IAPS, whereas countries like Kazakhstan, Uzbekistan, and Bhutan have realized the threats that IAS pose to their biodiversity, agriculture, and economy but still lack formal policy, plans, and programs. Nevertheless, countries including South Korea, Japan, Thailand, the Philippines, Malaysia, India, China, Russia, and Nepal have maintained database of IAS in their countries.

Other than controlling IAPS, countries are undertaking activities to prevent IAS entering their countries by developing and implementing quarantine regulations (e.g., Mito and Uesgi 2004; Son et al. 2009; Ju et al. 2012). Inspections have been strengthened at all borders and ports in many countries. For example, in Kazakhstan, there are some measures to control pests and diseases in agriculture under plant protection and plant quarantine programs. Border control measures have also been strengthened in North Korea and Japan. In China, many professional research teams, offices, and centers on IAS have also established in universities, research academies, and government agents (Ju et al. 2012; Yan et al. 2012).

Most of the policies and programs to control and manage IAS set by the Asian countries were either guided by or aligned with Aichi Biodiversity Target 9. The Target stated that by 2020, IAS and pathways were to be identified and prioritized, priority species were to be controlled or eradicated, and measures were to be in place to manage pathways to prevent their introduction and establishment (www.cbd.int/sp/targets/). Despite some successes to manage IAS in some Asian countries and progress made to formulate policies and implement programs and form institutions, a collective initiative at the continental and/or regional scale in Asia is urgently required because the Aichi goals have yet to be met. Given the interconnectedness among Asian countries through trade and travel, global as well as regional cooperation is essential to control and manage IAS. Therefore, it is high time for Asian countries to make a common regional strategy and take action against the threat posed by IAS on their environment and economy including human health. However, before the development of such a strategy, each country needs to identify management of IAS as a priority conservation issue, develop exclusive policies to deal with biological invasions, and designate offices and staff to implement policy decisions involving all stakeholders. In addition, continued funding to support such activities needs to be sought.

5.9 Conclusions and Way Forward

Hundreds of alien plant species are naturalized in Asia, with many of them being notorious invasive species of global significance. Yet, the knowledge base generated in the continent that is essential for IAPS management is insufficient and fragmented. For instance, most countries in this region do not have prioritized lists of IAPS endorsed by government authorities for management, though researchers have attempted to do so in a few countries like India (Mungi et al. 2019), Nepal (Tiwari et al. 2005; Shrestha et al. 2019a, b; Adhikari et al. 2021), and Turkey (Yazlik et al. 2018a). Biodiversity hotspots are shared between all countries in Southeast Asia with thousands of endemic plant species, but studies examining ecological impacts of IAPS are surprisingly lacking in this region. Similarly, ecological impact studies are also lacking in Central and North Asia. With the exception of a few estimates available for Southeast Asia, China, India, and Pakistan, economic cost valuation is not available for most of the species and countries in Asia. On top of the poor knowledge base, the national response (reactive) as well as the capacity (proactive) of most of the Asian countries to manage IAPS is low to medium (Early et al. 2016). Early Detection and Rapid Response (EDRR) is the most effective approach, after “prevention,” to manage biological invasions, yet this is the most neglected measure of IAPS management in Asia. In a nutshell, the number of IAPS is already high in Asia, and their number as well as spatial extent of their invasion is very likely to increase further in the near future due to lack of effective management responses (Early et al. 2016) and expanding international trade and economy of many countries in the continent (Seebens et al. 2015).

Increasing number of IAPS and their geographic extent of invasions not only threatens biodiversity and ecosystem services but also directly affects the livelihoods and well-being of millions, if not billions, of people in Asia. This necessitates some transformative approaches, as

mentioned below, which would prevent the introduction of new IAPS and mitigate the impacts of established IAPS. Since IAS do not recognize political borders, their management needs to extend beyond international borders. This could be possible through regional collaboration for research and information exchange among countries that share a common pool of IAS. While this kind of cooperation has already been successful to some extent in generating scientific knowledge, and subsequently managing IAS in Europe (DAISIE 2009), it is glaringly absent in Asia. International collaboration beyond Asia, such as the one that China and the USA have for the exchange of biological control agents against IAPS (Ding et al. 2006), needs to be promoted for effective management of plant invasions. Another important approach that needs promotion in Asia are biological control programs which are currently absent in many countries. Uncertain national funding and poor infrastructure including human resources together with low awareness among stakeholders have prevented many countries to initiate biological control programs (Day and Witt 2019). Research on biological invasions has traditionally focused on ecology, with socioeconomic dimensions poorly represented not only in Asia but also throughout the world (Vaz et al. 2017). Expanding biological invasions research to include socioeconomic dimensions of IAPS will help to generate socially relevant additional data and knowledge (Abrahams et al. 2019) that not only better inform the current management and policy decisions but also may better predict future invasions in an era of global environmental change (Kueffer 2010). The citizen science approach has emerged as an important tool for generating knowledge relevant to addressing the problems of biological invasions by tapping the potential of emerging information and communication technologies (August et al. 2015). This approach may help to narrow the geographic gaps in data availability through community engagement while disseminating useful information to communities themselves. Furthermore, lack of adequate awareness of the damage caused by IAS is a serious issue among most stakeholders, especially policy makers, for-

esters, agriculturists, and the general public. Major efforts are required to make all stakeholders adequately aware of the problem for the formulation of appropriate policies and implementation of effective management approaches.

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A Historical Perspective on Plant Invasion in Australia

6

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Abstract

Australia's separation from other land masses has resulted in the evolution of flora and fauna in relative isolation. The arrival of Europeans some 230 years ago marked the beginning of a mass invasion of the continent by alien plant (and animal) species from across the globe. These mass invasions have had profound effects on the Australian landscape and its native species and have required significant management interventions. In this chapter, we present an overview of the history of alien plant invasions in Australia and the scope of the current situation in terms of the number of species introduced. Seven case studies illustrate the nature of the invasive weed issues and the actions undertaken towards management. Case studies include Australian Weeds of National Significance (WoNS) (*Chrysanthemoides monilifera* subsp. *rotundata*, *Lantana camara*) and environmentally and agriculturally important invasive plants (*Opuntia inermis*, *Opuntia stricta*, *Echium*

plantagineum, *Cucumis myriocarpus*, *Citrullus lanatus*, *Andropogon gayanus*) as well as recent incursions (*Bassia scoparia*). Each case study outlines the impacts and risks associated with the invasion and presents the unique management approaches adopted - asset protection, biological control, successful eradication and ecosystem transformation. Several case studies draw comparisons between the establishment and persistence of alien plants in Australia and their native ranges and provide important clues on key traits that contribute to their successful invasion. Results to date have shown that the number of introduced plants to Australia has increased exponentially across most states and territories, particularly in recent years. Targeted control strategies for some WoNS such as *Chrysanthemoides monilifera* subsp. *rotundata* have been successful due to significant investment in the study of weed biology and physiology and subsequent development of effective integrated weed management strategies. The management strategies for several WoNS and invasive plants are evolving, through continued involvement of local, state and federal government and nongovernmental agencies and researchers to identify more effective control strategies. Lastly, future management challenges are described, including the expanding alien flora, the potential impact of climate change and risk manage-

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ment associated with weed incursion. Unique Australian insights can provide potential examples for other countries facing similar challenges as alien plants are now a global problem.

Keywords

Case studies · Climate change · Historical invasion patterns · Impacts · Invasion biology · Management · Weeds of national significance

6.1 Introduction

Australia is known for the unique and diverse native flora and fauna that have originated following a long period of isolation as an island continent. However, with the arrival of European settlers came many non-native plant species including both deliberate (i.e. crops) and accidental introductions. These initial introductions of alien plants from Europe were followed by other introductions from across the globe. Many of the alien plants introduced to Australia have subsequently naturalised and spread over vast areas of the continent, where they pose significant impacts to the native Australian flora and fauna. These plants have invaded arid, tropical, temperate and alpine habitats and encompass all life forms (i.e. herbs, grasses, vines, shrubs and trees), and their management has required the development of a diverse array of approaches and strategies. This chapter presents a brief overview of the history of plant introductions in Australia and describes the factors influencing successful invasion and management responses through a series of case studies highlighting the unique aspects of the Australian context.

While the nature and scope of alien plant invasions have been documented globally (Pimentel 2011), the species, their impacts and effective management responses vary considerably between continents and countries. Multiple factors contribute to this variation including (a) the history of plant invasions in the region investigated (i.e. which species have been introduced,

the introduction date and country of origin or donor country (see Pyšek et al. 2021, Chap. 7)), (b) the invasiveness of individual species in each region (including their biology and traits), (c) the resilience of native ecosystems to invasion or individual alien plant species, and (d) the management strategy (including policy and legislation) developed and relative success of implementation. While there are commonalities among successful global invaders, unique aspects of alien plant invasions on each continent are frequently associated with regional variation. This chapter therefore explores plant invasion and management from an Australian perspective.

6.1.1 History of Plant Invasions in Australia: An Overview

Pre-1788

Records and evidence of plant invasions prior to the European colonisation of Australia in 1788 are scarce. However, three potential sources of plant invasions during this period of Australia's history have been described. These include (i) natural invasions, (ii) anthropogenic activity of Aboriginal (and Torres Strait Islander) people, and (iii) other travellers to Australian shores.

- (i) *Natural invasions* (i.e. without human assistance) – Joseph Hooker described the Australian flora [from the essay 'On the Flora of Australia' (1859)] as containing three distinct elements: (1) an Australian or autochthonous element (being mainly endemic and near endemic species, many of which are xeromorphic), (2) an Antarctic element (i.e. species like *Nothofagus*) and (3) an Indo-Malayan element (i.e. tropical and subtropical rainforest assemblages). The characterisation of these three elements led to the idea of 'mass invasions' in Australia's past, although the nature of these invasions was undefined (Beadle 1981). Based on the theory of continental drift, Beadle (1981) provided more conclusive evidence for the origins of the Australian flora based on three main

phases: (a) the ancient Gondwanaland flora; (b) the xeromorphic flora, originating from Gondwanan lineages; and (c) the arid zone flora which is derived from Gondwanan lineages, xeromorphic taxa and littoral taxa, although some elements of the Australian flora must have originated outside of Australia to account for the numerous taxa of Southeast Asian origin (Beadle 1981). However, Australia has only been sufficiently close enough for biotic exchange with Asia to have occurred in the past 15 M years, with migratory routes possibly occurring only in the last several million years (Smith 1986). For example, two species of the widespread northern hemisphere genus *Rhododendron* (*R. viriosum* and *R. lochiaie*) occur in Australia, both of which are restricted to northern Queensland and are believed to have spread as a result of this biotic exchange (Smith 1986). Analysis of the flora of northern Australia (i.e. above 15°S latitude) revealed that about 28% of the 2220 species also occur outside of Australia (Specht and Mountford 1958). Other natural invasions to Australia include the many ‘cosmopolitan’ coastal species which are widespread across the Indian and Pacific Ocean countries and islands (e.g. *Cakile edentula*) and are likely to have dispersed through ocean currents (see further discussion by Groves (1986)).

- (ii) **Aboriginal people** – The arrival of Aboriginal people over 50,000 years ago in Australia does not appear to have been associated with any significant plant invasions (Groves 1986). This is possibly not surprising given the Aboriginal people’s close affiliation to the environment, as alien plants are likely to conflict with their cultural connection to the land (Smith 2002). In addition to the Aboriginal people, the Torres Strait Islanders are an indigenous group of people who occupied northern Queensland and at least 38 islands in the 150 km Torres Strait between the northern tip of Australia and the southern coast of Papua New Guinea. While
- there is no documented evidence that the Torres Strait Islanders introduced plant species into Australia, they regularly travelled between Australia and Papua New Guinea, and thus it is highly likely that some plants could have been dispersed over time. However, certain animals, including dingo (*Canis familiaris dingo*), have now been dated in terms of their arrival to this continent to be linked with migrating human populations. In 2020, the first whole genome sequencing of the dingo and the New Guinea singing dog was undertaken. It indicated that the ancestors of these two dogs arose in Southeast Asia around 9900 YBP (years before present) and reached Australia 8300 YBP. Given the approximately 150 km of ocean containing numerous islands between Papua New Guinea and Australia, it is assumed that both flora and fauna could have arrived with migrating peoples at that time (Zhang et al. 2020). Phylogenetic studies employing molecular markers such as nuclear, chloroplast and mitochondrial genes as well as whole genome sequencing will certainly assist in determining invasion routes and approximate time of introduction in future population studies (Zhu et al. 2019).
- (iii) **Other groups of visitors to Australian shores** – The Makassans, from the region of Sulawesi in modern-day Indonesia, were regular visitors to northern Australia between 1700 and 1900 collecting *trepang* (or sea cucumber). They are believed to have brought tamarind (*Tamarindus indica*) during these visits, which subsequently naturalised and spread (Macknight 1976). Tamarind is suspected to be the first naturalised plant in Australia as a result of human activities (Groves 1986). While many European [mostly Dutch] explorers mapped significant parts of the Australian coastline following Willem Janszoon’s ‘accidental’ discovery of Australia in 1606 (which he thought at the time was New Guinea) (Peters 2006), there is no formal or written evidence of plant invasions linked to these explora-

tions. However, given the number of expeditions to Australia and the level of European activity in the region just north of Australia, transportation of alien plants during these maritime expeditions undoubtedly occurred (Bean 2007). A number of non-native plant species have been recorded from Timor and Indonesia with origins that pre-date European migration to the region (Bean 2007). Currently, evidence suggests that visitors from southern Asia travelled to the Australian mainland well before 5000 BCE (before the Common Era) based on the presence of archaeological artefacts (see Bowdler 2002), but their role in the dispersal of non-native plants is currently unknown. Bean (2007) argues that it is highly likely there was an alien flora present in Australia prior to European arrival. He hypothesised that some of the plant species collected in 1770 by the European botanists Banks and Solander, combined with specimens from other early botanists, may not be indigenous to Australia based on several key characteristics (i.e. invasive elsewhere, occur beyond natural dispersal limits, form disjunct populations, etc.). Following examination of early collections, Kloot (1984) concluded that about 100 plant species could have naturalised in Australia prior to European arrival. Bean (2007), however, suggests that this number could be much higher.

Post-1788

The arrival of the First Fleet in 1788 saw the deliberate [and documented] introduction of many new plant species to Australia. While most were of agricultural importance (i.e. crops and fruit trees), numerous potentially invasive alien species including coffee (*Coffea arabica*), guava (*Psidium guajava*), bamboo (subfamily Bambusoideae – exact species not documented), prickly pear (*Opuntia* sp.) and Spanish reed (*Arundo donax*) were introduced. The first reliable documented account of naturalised plants in Australia comes from Robert Brown who recorded 29 non-native plants growing around Sydney between 1802 and 1804 (Groves 2002),

although not all were considered to be ‘weedy’ at the time. Subsequently, nearly all have become widely naturalised (Groves 2002). Following Brown’s account, botanists and naturalists continued to compile lists of naturalised plant species, initially for specific regions and later the individual states and territories (Fig. 6.1). However, it was not until the late 1980s that the first complete national list of naturalised plants was produced (Table 6.1). Since European settlement, the number of alien plant species introduced to Australia has exceeded 29,000 of which approximately 10% (>3000) have become successfully naturalised (Table 6.1). Interestingly, the number of vascular plants introduced into Australia exceeds the number of native vascular plants by 7750 (Table 6.1). Additionally, the recent rate of plant naturalisations has accelerated (see Fig. 6.1). Groves and Hosking (1998) identified 295 taxa that naturalised in Australia over a 25-year period (1971–1995). Dodd et al. (2015) showed the increase in naturalisation rates to be linear over the period 1880–2000, based on herbaria collections of naturalised plants as a proportion of total herbarium collections. It must be noted that the alien flora held in many herbaria across Australia is likely to be an underrepresentation of the actual number, as alien specimens are generally or routinely not collected by trained botanists.

The significant increase in the number of naturalised plants reported between 1990 and 1997 may be attributed to the inclusion of species from various compiled data sources rather than an actual time step increase in numbers during this period (Fig. 6.1; Table 6.1). Furthermore, citizen science websites such as Canberra Nature Map (CNM: <https://canberra.naturemapr.org/>) for the Australian Capital Territory (ACT) have led to a proliferation of reports on new naturalisation rates, which are also not reflective of information supported by historic herbaria collections. For example, analysis of CNM records showed that between 2015 and 2019, over 570 alien plant species (spanning 3800 records/sighting) were reported through CNM, including many species previously not reported in the ACT (Mulvaney unpublished data).

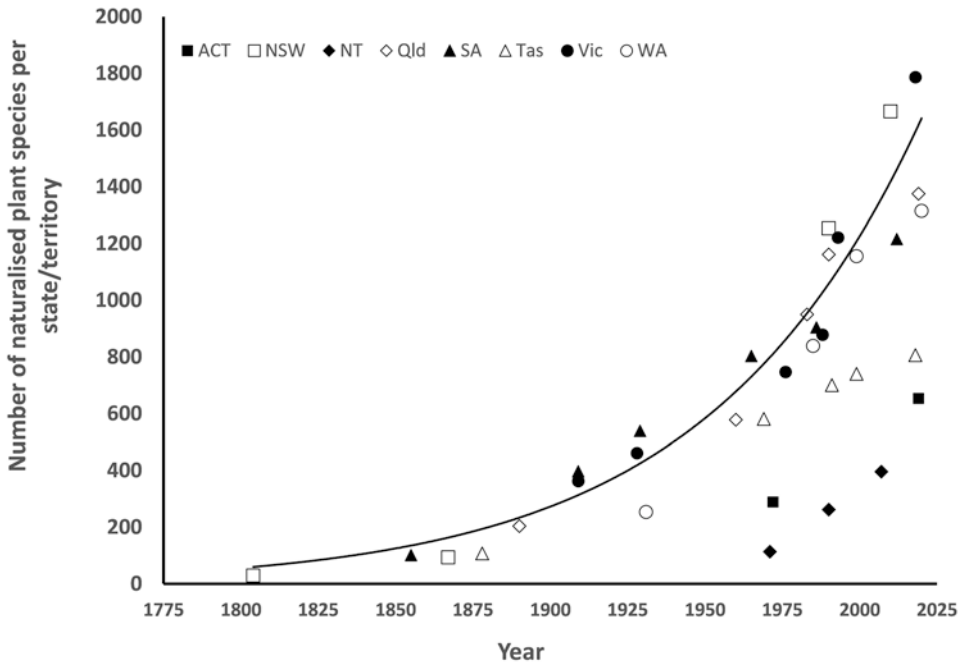


Fig. 6.1 An estimate of the number of naturalised plant species introduced over time for each Australian state/territory. Data collated from published records of naturalised plant species. ACT = Australian Capital Territory, NSW = New South Wales, NT = Northern Territory,

Qld = Queensland, SA = South Australia, Tas = Tasmania, Vic = Victoria and WA = Western Australia. The overall trend line is also presented (note: trend line presented is not representative of the mean value across all states territories as they differ in size and invasion history)

Table 6.1 The estimated number of alien plant species introduced and naturalised in Australia (national total)

Year	Number of alien plant species introduced	Number naturalised	Native species	References
1990	n/a	1952 [^]	15,638	Hnatiuk (1990)
1997	n/a	2733 [#]		Lazarides et al. (1997)
2003	n/a	2681		Groves et al. (2003)
2007	26,242	2739		Randall (2007)
2009			21,645	Chapman (2009)
2017	29,387	3027		Randall (2017)

[^]Note Hnatiuk (1990) is based solely on herbarium records and thus is likely to be an underrepresentation

[#]This number included species, subspecies and varieties; the number of species cannot easily be determined from this text

The largest proportion of naturalised flora in Australia originated from Europe (47.4%), followed by the Americas (29.9%), Africa (14.3%), Asia (6.3%) and Oceania (2.1%), with an increasing number of source countries reported over time (Dodd et al. 2015). Initially, plant introductions originated mainly from Europe and Africa, a reflection of the actual trading routes and maritime passages (Groves 1986). The majority of naturalised plant species were imported to Australia originally as ornamental plants (66%) (Groves

et al. 2005), with fewer introduced for agricultural purposes (7%); these findings are consistent with similar assessment in other countries like the USA and Canada. In one assessment, Lonsdale (1994) documented 463 grasses and legumes which were introduced into northern Australia between 1947 and 1985 for pasture improvement. Although only 21 were eventually recommended for use, approximately 60 have subsequently become invasive. Given that 94% of all alien plants introduced into Australia (n = 26,242) were introduced through

the gardening [ornamental] sector (Virtue et al. 2004), and many of the naturalised ornamental plant species examined were available for sale (Groves et al. 2005), the contribution of this sector to the increase in environmental weeds in recent years is significant (Table 6.2).

In response to the arrival of a large number of invasive alien plants in Australia, the Commonwealth Government released the first National Weeds Strategy in 1997 (ARMCANZ et al. 1997). A key goal of this strategy was ‘to reduce the impact of existing weed problems of national significance’. To further address this goal, the Commonwealth Government took a species-led approach to prioritise 20 Weeds of National Significance (WoNS) in 2000, from a list of 71 major invasive plant species nominated by a range of experts (see Thorp and Lynch 2000). Significant investment and resources were then directed towards these 20 WoNS, including dedicated coordinators, national management groups, creation of national strategies, best practice management manuals and specific funding for a wide range of on-ground management activities and research priorities (e.g. biocontrol and ecological studies). Significant outcomes were achieved in the management of the 20 species selected (see several examples in case studies below). However, management of other nationally significant invasive plant species was put at a distinct disadvantage as a consequence of not being listed as a WoNS. In some cases, these species were not ranked as WoNS as information on their ecology and impacts were either poorly understood or documented.

Given the growing evidence pointing to the need of urgent national management of other species, an expanded list of 32 WoNS species was released in 2012 (the actual number is higher as several listings are groups of weeds, e.g. bitou bush/boneseed, brooms, Opuntoid cacti and aspar-

agus weeds) (Table 6.3). Specifically, invasive vines were highlighted as a rapidly increasing problem following the publication of several Biology of Australian Weeds research articles (e.g. *Anredera cordifolia* (Vivian-Smith et al. 2007)). This recognition led to invasive vines being listed as a *Key Threatening Process* under the NSW Threatened Species legislation and subsequently their listing in the second group of WoNS (see Table 6.3).

Despite the creation of the WoNS programme and its successes, there are still many nationally important invasive plant species not encompassed by the WoNS programme. Many of these non-WoNS species were considered to be significant invasive alien species for decades (see non-WoNS case studies in Sect. 6.3). For example, during the first Australian Weeds Conference held in 1954, research papers were presented on nine species - three would go on to become part of the initial 20 WoNS (*Rubus fruticosus*, *Lantana camara* and *Nassella trichotoma*) and a fourth in the expanded list (*Lycium ferocissimum*). The remaining five species (*Phragmites australis*, *Senecio jacobaea*, *Chondrilla juncea*, *Oxalis pes-caprae* and *Rosa rubiginosa*) are still considered to be major invasive alien species today. Raising their profile and highlighting their impacts will require more than just research into their ecology and biology, as it is unlikely that every nationally significant invasive alien plant species in Australia can be accounted for under the single species WoNS approach. However, a focus on individual species can provide models for potential adoption for management of other invasive plant species (as highlighted in the case studies).

The case studies presented below represent a select group of invasive alien plant species chosen to illustrate the state of plant invasions in Australia and likely future directions for inva-

Table 6.2 Number of naturalised plant species and change relative to the type of alien plant between 2004 and 2017

Alien plant type ^a	Number of naturalised plants species		Increase	
	Virtue et al. (2004)	Randall (2017)	Species number (n)	Percentage (%)
Agricultural	954	977	23	2.4
Environmental	1765	1963	198	11.2
Total	2719	2940	221	8.1

^aRefers to the type of habitat invaded and thus the ‘type’ of alien plant (e.g. environmental weed)

Table 6.3 Invasive plant species in Australia assessed as Weeds of National Significance (WoNS)

Scientific name	Common name	Family name	WoNS ^a	First recorded date in Australia	Origin
<i>Alternanthera philoxeroides</i>	Alligator Weed	Amaranthaceae	1	1946	South America
<i>Andropogon gayanus</i>	Gamba Grass	Poaceae	2	1931	Africa
<i>Annona glabra</i>	Pond Apple	Annonaceae	1	1886	Tropical America and West Africa
<i>Anredera cordifolia</i>	Maderia vine	Basellaceae	2	1906	South America
<i>Asparagus aethiopicus</i>	Ground Asparagus	Asparagaceae	1	late 1800s prior 1940 1870	Southern Africa
<i>Asparagus africanus</i>	Climbing Asparagus				
<i>Asparagus declinatus</i>	Bridal veil				
<i>Asparagus plumosus</i>	Climbing Asparagus -fern				
<i>Asparagus scandens</i>	Asparagus Fern				
<i>Asparagus asparagoides</i>	Bridal Creeper	Asparagaceae	1	1857	Southern Africa
<i>Austrocylindropuntia</i> spp.	Prickly pears	Cactaceae	2	1788	Americas
<i>Cylindropuntia</i> spp.					
<i>Opuntia</i> spp.					
<i>Cabomba caroliniana</i>	Cabomba	Cabombaceae	1	1967	North, South America
<i>Chrysanthemoides monilifera</i> subsp. <i>monilifera</i>	Boneseed	Asteraceae	1	1852 1908	Southern Africa
<i>Chrysanthemoides monilifera</i> subsp. <i>rotundata</i>	Bitou Bush				
<i>Cryptostegia grandiflora</i>	Rubber Vine	Apocynaceae	1	1875	Madagascar
<i>Cytisus scoparius</i>	Scotch broom	Fabaceae	2	c. 1800 1855	Europe
<i>Genista linifolia</i>	Flax-leaved Broom	Fabaceae			
<i>Genista monspessulana</i>	Montpellier Broom	Fabaceae		c. 1850	
<i>Dolichandra unguis-cati</i>	Cat's claw creeper	Bignoniaceae	2	1865	South America
<i>Eichhornia crassipes</i>	Water hyacinth	Pontederiaceae	2	1890s	South America
<i>Hymenachne amplexicaulis</i>	Hymenachne	Poaceae	1	1970	South America
<i>Jatropha gossypifolia</i>	Bellyache bush	Euphorbiaceae	2	late 1800s	Central-South America
<i>Lantana camara</i>	Lantana	Verbenaceae	1	1841	Central-South America
<i>Lycium ferocissimum</i>	African boxthorn	Solanaceae	2	mid-1800s	Southern Africa
<i>Mimosa pigra</i>	Mimosa	Fabaceae	1	1870s	South America
<i>Nassella neesiana</i>	Chilean needle Grass	Poaceae	1	1934	South America
<i>Nassella trichotoma</i>	Serrated tussock	Poaceae	1	c. 1900	South America
<i>Parkinsonia aculeata</i>	Parkinsonia	Fabaceae	1	c. 1800s	Northern, Central, South America
<i>Parthenium hysterophorus</i>	Parthenium	Asteraceae	1	late 1950s	Northern, Central, South America
<i>Prosopis</i> spp.	Mesquite	Fabaceae	1	c. 1880s	Central America
<i>Rubus fruticosus</i> aggregate	Blackberry	Rosaceae	1	c. 1840s	Europe
<i>Sagittaria platyphylla</i>	Arrowhead	Alismataceae	2	1959	Northern America

(continued)

Table 6.3 (continued)

Scientific name	Common name	Family name	WoNS ^a	First recorded date in Australia	Origin
<i>Salix</i> spp. (except <i>S. babylonica</i> , <i>S. x calodendron</i> , <i>S. x reichardtii</i>)	Willows	Salicaceae	1	Early 1800s	Europe
<i>Salvinia molesta</i>	Salvinia	Salviniaceae	1	1950s	South America
<i>Senecio madagascariensis</i>	Fireweed	Asteraceae	2	1918	Madagascar, southern Africa
<i>Solanum elaeagnifolium</i>	Silver-leaved Nightshade	Solanaceae	2	1909	Central and southern North America
<i>Tamarix aphylla</i>	Athel pine – Tamarisk	Tamaricaceae	1	1930s	Northern Africa, middle east, South Asia
<i>Ulex europaeus</i>	Gorse	Fabaceae	1	1830s	Europe
<i>Vachellia nilotica</i>	Prickly acacia	Mimosaceae	1	1890s	Africa, Middle East

^aWoNS (Weeds of National Significance), 1 = the initial 20 species listed in 2000, and 2 = the additional species listed in 2012

sive plant management. We present examples of invasive alien plants that have seriously impacted the Australian landscape and led to the development of critical management strategies for their reduction or eradication. In some cases, eradication has been successful, while in others the invader continues to be a significant threat. Australians have typically employed various strategies for management, including assessment of the risk to prioritise investment in management, use of biological control agents to control widespread species with significant impacts and the successful integration of chemical, physical and cultural management strategies over time for reduction of propagules and seed banks.

6.2 Case Studies: Weeds of National Significance

6.2.1 Bitou Bush (*Chrysanthemoides monilifera* subsp. *rotundata*)

The South African plant *Chrysanthemoides monilifera* subsp. *rotundata* was likely accidentally introduced into Australia in the early 1900s, where it subsequently established and spread. In the 1950s, however, it was deliberately planted

along large sections of the New South Wales (NSW) coast to stabilise and revegetate sand dunes after mining for a range of minerals. By the 1980s there was growing concern about its invasive potential and significant threat to native plants. In 1999 it was listed as a Key Threatening Process (KTP) under the NSW threatened species legislation and as a WoNS in 2000.

In addition to the WoNS programme, the NSW Government released a Threat Abatement Plan (TAP) for the species in 2006 to meet the requirement of the KTP listing. The TAP identified 150+ plant species and 24 ecological communities that were directly threatened. The TAP established a new management approach for invasive plant species that threaten biodiversity, in that the native species threatened by *C. monilifera* subsp. *rotundata* were identified along with sites where control would lead to a conservation outcome (see Downey 2010). Over the proceeding 10+ years since the TAP was released, control of *C. monilifera* subsp. *rotundata* has occurred at 110+ priority sites outlined in the TAP across coastal NSW providing protection to over 95% of the plant species threatened. The TAP was supported by the broader WoNS programme which included containment zones, a comprehensive biocontrol programme and community education and awareness campaign and control in other priority areas as

well as the development of best practice guidelines and management. The WoNS programme also included a range of initiatives and management outcomes for the closely related *C. monilifera* subsp. *monilifera* (Boneseed) which is also a major invasive plant species in Australia and jointly a WoNS species. Additionally, the other four subspecies not present in Australia were banned from import based on their risk and invasive potential, a decision that was later supported through detailed modelling (Beaumont et al. 2014). Comparisons of native and alien range data can provide useful insights into management and our general understanding of why a particular species can become invasive as an alien. For example, Beaumont et al. (2014) showed that the climatic envelope for *C. monilifera* subsp. *monilifera* in Australia was significantly greater than in its native range, in part because the southern latitudes where it is invasive in Australia and New Zealand are not present in South Africa.

6.2.2 Lantana (*Lantana camara*)

Lantana camara is a woody shrub originating in South and Central America and was introduced into Australia for ornamental purposes in 1841. Shortly thereafter it escaped cultivation and spread extensively, but it was not until the early 1900s that active management was advocated and initiated. It is now estimated to have invaded over 5 M hectares in Australia, including pastures, croplands and native habitats. Despite 100+ years of active management, these efforts have been largely unsuccessful, as is the case in other parts of the world (Bhagwat et al. 2012).

The first biocontrol agent was released on *L. camara* in Australia in 1916. Despite the release of 26 other agents over the past 100 years, successful control has not been achieved (Palmer et al. 2010). Genetic analysis of *L. camara* revealed that the species is a ‘complex’, as no recent records of parental species could be identified. Instead, the current ‘species’ is the outcome of extensive hybridisation combined with polyploidy/polyploidisation within and between wild, cultivated varieties, and naturalised taxa (Goyal

and Sharma 2015). Such significant genetic variation may limit successful implementation of a host-specific biocontrol agent as the ‘species’ is unlikely to exist in the native range.

As outlined above, given the area invaded by *L. camara* and its residence time in Australia and the fact that broad-scale control or eradication is unlikely, one of the major WoNS initiatives was the development of a national plan to protect assets at risk from *L. camara* invasion (see BQ 2010). This asset-based approach is based on the Australian government’s biosecurity model for all alien species in Australia in which management is based on a theoretical generalised invasion curve of residence time relative to area invaded overlaid with four standard management objectives (prevention, eradication, containment and asset protection) (EWWG 2007). Prior to the development of the national plan, the biological assets threatened by *L. camara* invasion were thought to be limited to specific species, or areas, despite acknowledgement of broader more significant potential impacts (e.g. Gentle and Duggin, 1997).

Two major approaches were adopted to determine the biodiversity threat. Firstly, a range of rapid assessments was undertaken from invaded and non-invaded sites across southeastern Australia which showed an impact threshold effect of *L. camara* density on native species. The threshold varied for various plant communities; however, the greater the cover of *L. camara*, the lower the species richness of native species (Gooden et al. 2009). Secondly, an assessment (using a modified version of the methodology developed for *C. monilifera* subsp. *rotundata*) was used to determine the biodiversity at risk (see case study 6.2.1 for details). This assessment revealed that *L. camara* threatened 1321 native plant species, 158 native animal species and 150+ ecological communities. Of these, 275 native plant and 24 native animal species required immediate protection nationally (Turner and Downey 2010). The identification and prioritisation of specific species at risk from *L. camara* invasion enabled evaluation of individual sites and targeted conservation efforts on areas of greatest need and likelihood of achieving a

successful outcome using a conservation triage approach (Downey et al. 2010a).

Apart from threatening native biodiversity, *L. camara* has been reported as poisonous to domesticated animals (e.g. sheep, cattle, buffalo and guinea pigs). The liver and kidneys of animals that consume *L. camara* typically exhibit a characteristic increase in serum glutamic-oxaloacetic transaminase activity and hepatic and renal xanthine oxidase activity, resulting in obstructive jaundice and subsequent photosensitisation (Sharma et al. 1981). Leaves and stems of *L. camara* have exhibited nematicidal properties that could also potentially assist in its invasion success (Begum et al. 2008) and may potentially provide lead molecules for the development of bionematicides (Udo et al. 2014) and biofungicides (Singh and Srivastava 2012).

Many invasive plant species with successful invasion tendencies have also been noted to possess strong allelopathic potential. *Lantana camara* shows potential for allelopathic activity resulting in reduced vigour in native plants, thereby reducing native biodiversity and disrupting succession within invaded habitats (Gentle and Duggin 1997; Day et al. 2003). Similar inhibitory effects of *L. camara* and its residues were also observed on vegetable crops (e.g. Chinese cabbage, chilli and rape seed (Sahid and Sugau, 1993). While the phytotoxic activity of *L. camara* has been reduced over time through vermicomposting of residues (Hussain et al. 2016), its unique allelochemical composition has proven effective for the control of another invasive alien species, water hyacinth (*Eichhornia crassipes*) (Saxena 2000). Chemical defences resulting in allelopathic potential have been shown to play a role in plant invasion success (Latif et al. 2017) and in the case of *L. camara* may also contribute to its persistence.

6.3 Case Studies: Weeds Not of National Significance

6.3.1 Prickly Pear (*Opuntia inermis* and *Opuntia stricta*)

The WoNS programme described previously in this chapter was not the first nationally significant species-led programme in Australia. Eighty years

earlier the Australian Government initiated the Commonwealth Prickly Pear Board in 1920 in response to the enormous scale of the prickly pear (*Opuntia inermis* and *Opuntia stricta*) invasion (Dodd 1940). Prickly pear species were first introduced to Australia in 1788 with the arrival of Europeans, but it was not until ~1900 that the species was reported to be spreading rapidly, and by 1913 it was reported to have infested over 6.3 M hectares. At the peak of invasion in 1925, it was estimated that prickly pear had spread over 24 M hectares, half of which was so infested that it was unable to be grazed by livestock. Many farming properties were subsequently abandoned as the cost of mechanical and chemical control was economically impracticable, exceeding the value of the land by over 20-fold. At its peak, the densities of prickly pear were estimated at 16,000 plants per hectare with an estimated biomass of 250,000 kilograms (kg) per hectare (Dodd 1940).

In the 1920s, the Prickly Pear Board was established with the express purpose of finding an effective biological control agent. The Prickly Pear Board introduced the cactoblastis moth (*Cactoblastis cactorum*) into Australia in 1925, and it was released after mass rearing in early 1926. By 1930 some 3 billion eggs had been reared and released throughout eastern Australia. The biocontrol agent was so successful that large-scale destruction of prickly pear was observed by 1933. However, this initial success was followed by mass reductions of the moth population due to low prickly pear densities. In subsequent years, prickly pear densities rebounded due to a lack of the biocontrol agent. The moth numbers subsequently recovered, and by 1939 comprehensive control was achieved enabling abandoned land to be reclaimed. The cost of the 19-year programme was AUD£168,600 [equivalent to AUD\$12 M in 2019], providing a perspective on the expenses required for the successful management of this invasive plant species (Dodd 1940). Today, prickly pear is still observed across eastern Australia, but at much reduced numbers, and is typically eradicated where possible by spot spraying of herbicides. Although prickly pear infestation has generally been kept under control, a large number of other opuntoid cacti have become significant invasive plant species in

Australia in recent years, leading to their inclusion in the second WoNS list. Interestingly, Cactaceae is only one of two major plant families absent from the Australian flora (Beadle 1981).

6.3.2 Paterson's Curse (*Echium plantagineum*)

Echium plantagineum is an invasive annual herbaceous plant that was introduced into Australia in the 1840s from Europe. It was initially dispersed as an ornamental plant across southern Australia due to its impressive floral display of deep purple flowers. It readily escaped, and by the 1890s through several additional dispersal pathways (e.g. livestock and contaminated hay), it became widely established across large tracts of south-eastern Australia and southern Western Australia (Piggin and Sheppard 1995). Today *E. plantagineum* has spread throughout every state and territory and invaded over 30 M hectares, forming dense purple monocultures in early to late spring when in bloom, particularly in years with optimal rainfall following a prolonged drought.

Invasion success of this species has been attributed to a range of traits including elevated genetic diversity, tolerance to a range of environmental conditions encountered across Australia (i.e. low rainfall and extreme temperatures to higher elevation and low temperatures), the production of bioactive secondary metabolites supporting improved plant defences (Zhu et al. 2017) and prolific seed set and seed dormancy (Piggin and Sheppard 1995).

Studies comparing plant demography between Australia and the native European range (i.e. Iberian Peninsula in Spain and Portugal) showed that *E. plantagineum* seedling establishment was two to five times greater in Australia and that seed bank incorporation also was three times higher leading to a greater abundance as an alien in Australia (Grigulis et al. 2001). *Echium plantagineum* is self-incompatible in the native range, but self-compatible in its invaded territory of Australia (Petanidou et al. 2012), potentially enhancing the ability to colonise and spread. In direct contrast to the less invasive congeneric alien plant species, *E. vulgare*, *E. plantagineum*

exhibits significantly higher genetic diversity across its genome and possesses a smaller genome size (Zhu et al. 2017). Small genome size has also been associated with enhanced competitive ability and modification of morphological and physiological traits such as larger leaf area and higher photosynthetic rates owing to the reduced allocation of carbon resources for cell cycling (Bennett et al. 1998).

Apart from its physical adaptations for growth in extreme conditions, *E. plantagineum* has been shown to contain an arsenal of chemical defences that assist in its defence against other plants, pathogens and insect/mammalian herbivores. Aerial tissues of the plant contain high concentrations of pyrrolizidine alkaloids and their N-oxides (Skoneczny et al. 2019). These metabolites deter certain insect herbivores and have also been shown to be associated with livestock toxicity (Molyneux et al. 2011). The alien congener *E. vulgare* also contains pyrrolizidine alkaloids albeit at relatively lower concentrations (Skoneczny et al. 2017). The roots of *E. plantagineum* produce and release phytotoxic naphthoquinones, including acetylshikonin and shikonin, which have both been shown to be inhibitory to germinating alien plant seedlings and growth of mammalian cells (Durán et al. 2017). The biosynthesis of phytotoxic naphthoquinones (shikonins) in *E. plantagineum* is also upregulated in roots exposed to higher temperatures and under short-term drought conditions (Weston et al. 2013; Skoneczny et al. 2019).

Echium plantagineum was ranked 32nd in the assessment of the Australian Weeds of National Significance (WoNS) out of 71 weeds species nominated, despite being ranked as having the second highest cost of control and the third highest current distribution and ninth highest potential distribution and posing a significant threat to grazing livestock and land values (see Thorp and Lynch 2000). It was also not ranked as a WoNS in the second round in 2012, despite being a nationally significant invasive plant species, possibly due to the fact that management can be achieved in many cases with the application of a variety of cost-effective herbicides.

In Australia, the status of *E. plantagineum* can be contentious, with research showing both nega-

tive impacts on crop and pasture lands but positive value for beekeepers and for its use in cosmeceuticals and biomedicinals (Piggin and Sheppard 1995; Durán et al. 2017; Skoneczny et al. 2017). This conflict among diverse stakeholder groups has had a lasting legacy and has contributed to the current legislation and policies for its biological control in Australia.

The initiation of a biological control programme for *E. plantagineum* began in 1971 with agreement among state agricultural departments with biocontrol research programmes supported for many years. However, in 1978 the programme was challenged by apiarists who believed that the release of biocontrol agents would destroy a ‘valuable’ potential source of nectar for production of honey. The conflict lasted several years and involved multiple reviews/inquires, prolonged and protracted negotiations and finally legal proceedings, and as a result, the biocontrol programme was halted in 1983. The outcome of this conflict and a key resolution was the development and passage of the Commonwealth *Biocontrol Act 1984* to ensure that conflicts relating to the release of biocontrol agents in Australia could be administered through a legislative instrument and framework (Cullen and Delfosse 1984). Another key measure to resolving the conflict was a report on the economic status that showed the annual management costs in the state of Victoria alone at AUD\$ 3.2 M compared with an annual benefit of AUD\$ 900,000 (Field et al. 1986). In 1988 the biocontrol programme was subsequently reinstated, and six agents were released with limited conflict or opposition (see Piggin and Sheppard 1995). Today, several of these agents can be found in high abundance across southern Australia (primarily the leaf beetles and stem/crown weevils) (Weston et al. 2012).

6.3.3 Prickly Paddy Melon (*Cucumis myriocarpus*) and Camel Melon (*Citrullus lanatus*)

Cucumis myriocarpus and *Citrullus lanatus* are annual invasive species in the Cucurbitaceae family and were introduced into Australia in the early to mid-1800s from sub-Saharan Africa.

While *C. myriocarpus* was potentially introduced unintentionally, *C. lanatus* was introduced deliberately as a feed species for camels that were used at the time to transport construction materials to build roads and railways (Barker 1964). Both species are now considered significant invasive plants in broadacre and mixed cropping agricultural zones. Recently, Llewellyn et al. (2016) described them as major invasive alien species in summer grain crop rotations and fallows in Australia, and Borger et al. (2018) listed *C. myriocarpus* as a major problem in the Western Australian wheat belt. Both species are also invasive in natural ecosystems across drier inland regions of Australia where they pose a threat to native species (Hallett et al. 2014).

These introduced melons exhibit a similar range of traits that potentially contribute to their invasive ability and impact (Shaik et al. 2017). Such traits include seed dormancy, high seed production, drought tolerance, ability to be pollinated by non-specific pollinators (in the case of *C. lanatus*) and toxicity to some animal herbivores (i.e. horse, sheep and cattle deaths have been reported). Furthermore, both species have shown potential for allelopathic activity through the production of cucurbitacins and other unknown metabolites and have exhibited antimicrobial and nematocidal activity on soil organisms (Hao et al. 2007; Mafeo and Mashela 2010; Harrison et al. 2012).

Camel and prickly paddy melons can also be prodigious seed producers when irrigated or adequate soil moisture is available. Seeds of each species frequently exhibit dormancy which results in multiple ‘pulses’ of germination from early spring through to mid-summer depending on availability of soil moisture through rainfall or irrigation. The mucilaginous seed coats can adhere to vehicles and grazing animals aiding in seed dispersal, and parrots, particularly galahs, can also impact seed dispersal. The adaptability of *C. lanatus* to varied climatic conditions also supports its successful invasion across Australia (Ramirez et al. 2014). The ability of both melon species to produce adventitious roots under waterlogged conditions may also support its adaptation to regions experiencing flooding

events in arid, subtropical and temperate climates (Shaik et al. 2016a).

Recent studies have shown that Australian populations of *C. myriocarpus* and *C. lanatus* exhibit limited genetic diversity, with each species represented by a single genotype in Australia (Shaik et al. 2015; Shaik et al. 2016a; Shaik et al. 2016b). This observed lack of genetic diversity may favour the eradication of these weeds using host-specific biological control agents. However, considerable research efforts are required to ascertain feasibility of introduction of biocontrol agents, given their genetic similarity to economically important melon species (e.g. watermelon). The recent recognition of the ecological and economic impacts of these invasive melons (e.g. Llewellyn et al. 2016) combined with recent studies on their phenology and biology (Shaik et al. 2017) has led to a reassessment of their risk level and status as major invasive plants in drier inland regions of Australia. Prior to this, the melons were considered to be low-priority alien plants of roadsides, railways corridors, stockyards and other disturbed sites (*C. lanatus*) and cultivated crops (*C. myriocarpus*). Recognition of their invasive status is likely to lead to improved management outcomes that are aligned to the actual risk and impact posed.

6.3.4 Gamba Grass (*Andropogon gayanus*)

Andropogon gayanus is an African C_4 grass species which was introduced into Australia deliberately as a pasture grass in 1931. It subsequently invaded large tracts of pastureland in northern Australia (Queensland and Northern Territory), and areas with eucalypt open forest, woodland and savannas (Rossiter et al. 2003). Unlike the native grasses which are less than 0.5 m in height, *A. gayanus* grows to over 4 m, producing over four times the biomass of native grasses (up to 1.7 kg per m²). The increased height and biomass of *A. gayanus* in invaded sites result in altered fuel loads and increased intensity of bush fires (Rossiter et al. 2003). Rapid changes in ecosystem services illustrate how the grass-fire cycle

(D'Antonio and Vitousek 1992) has enabled *A. gayanus* transformation of invaded ecosystems, particularly with respect to understorey composition across northern Australia.

By modification of grass-fire cycles (i.e. due to its high biomass accumulation), *A. gayanus* has transformed ecosystems across northern Australia. In addition, production of 7 times more shoot N and 2.5 times greater root N compared with native grasses has altered soil N cycle. It also stimulates soil ammonification processes (Rossiter-Rachor et al. 2009) and affects soil moisture availability in invaded sites, with a tripling of water usage and a halving of deep-water drainage compared to uninvaded native grass sites (Rossiter et al. 2002). *Andropogon gayanus* invasion has also resulted in reduced tree canopy cover leading to mortality of certain native tree species (see Bowman et al. 2014). While such changes have significantly altered the grassland ecosystems of northern inland Australia, invertebrate composition between invaded and uninvaded sites has not yet been reported to be affected (Parr et al. 2010).

Seed biology of *A. gayanus* may also contribute to the invasion success of this weed in northern Australia. Bebawi et al. (2018) noted that seed persistence is supported by deeper burial of the seed, relative to shallow placement of seed which leads to loss of viability within 1 year of seed shedding in dry tropics of northern Australia. *Andropogon gayanus* typically germinates and persists well in cooler climates and has strong potential to expand across southern parts of Australia, particularly if predicted changes in Australia's climatic zones are realised.

At this time, suitable management strategies for the vast areas invaded by *A. gayanus* include controlled burning, herbicide application and replanting of native trees and understorey vegetation. However, intensive long-term management will be required across vast grazing areas in the northern Australia to limit the spread and manage the grass-fire cycle. This will require additional knowledge about the genetic variation among geographically dispersed populations and their ability to withstand fire and impact establishment of native species. The ability of *A. gayanus* to

transform vast tracts of northern Australia into fire-prone grasslands has led to the species being listed in the second group of WoNS in 2012.

6.3.5 *Kochia (Bassia scoparia)*

Bassia scoparia was introduced into Australia in 1990 as a forage plant for sodic soils and saline land rehabilitation in southeastern Western Australia. One year later it was sown at 68 sites over an 850 km area and soon naturalised; within 2 years it had dispersed from 60% of infested sites (Dodd and Randall 2002). Prior to initiation of the eradication programme in 1992, 38 of the 52 naturalised sites were < 10 ha in size, with the other 12 ranging in size up to 140 ha, with the total area invaded being 3277 ha in 1993 (Dodd and Randall 2002; Dodd 2004). In spite of the fact that the situation was considered challenging and not 'ideal' for achieving eradication (see Rejmánek and Pitcairn 2002), *B. scoparia* was successfully eradicated in the first nationally funded programme in Australia for a recent or new weed incursion.

Bassica scoparia exhibited several unique characteristics which made it an ideal candidate for successful eradication. Specifically, its distribution was limited and well documented, its seed is short-lived following dispersal (1–3 years with most germinating within 12 months) and although it spreads via wind-blown plants or 'tumble weeds', fences established to exclude grazing animals as part of the sowing rehabilitation programme were fortuitously successful in limiting its spread (Dodd and Randall 2002). These attributes supported the successful eradication of *B. scoparia* and contributed to it being an exceptional case (Panetta and Timmins 2004) as few other examples of plant eradication following establishment over such a significant area have been observed outside of islands.

By 2000, in less than 10 years, *B. scoparia* was considered to have been eradicated, responding positively to such efforts (herbicide, grazing, burning and mechanical removal) despite the broad scale of infestation, with most sites virtually free from infestation within 2 years (Dodd

2004). While its invasion history was unique, specific management responses aided the successful outcome including rapid response (eradication over a 2-year period) with state and federal funding made available to achieve a positive outcome (Dodd 2004). Both rapid response and multiple control tactics are typically required for the successful eradication of any alien plant (Panetta and Timmins 2004).

6.4 Summary of Case Studies

The case studies presented in this chapter illustrate that adopting a species-led approach in the form of the WoNS programme to manage invasive plant species in Australia has had some proven successes (i.e. the winners), but there have also been numerous failures or 'losers' with this approach (i.e. those non-WoNS species). While some of these non-WoNS were listed in the second round (e.g. *A. gyanus*), it is impractical to manage every invasive plant species in Australia under a species-led approach. However, the Australian WoNS programme has had significant benefits which have flowed on to the management of non-WoNS species. These include well-developed and broad-scale education and awareness campaigns, extensive development of best practice guidelines, the development of approaches to identify those native species at risk due to such threats and the assessment of risk management strategies for prioritisation of management or future investment in control strategies.

It should be noted that significant benefits to invasive plant species management have also occurred outside of the WoNS programme (i.e. the development of the Biocontrol Act; see the *E. plantagineum* case study). While the control of prickly pear has been a notable success in Australia as previously described, numerous other opuntoid cactus species have become highly invasive in recent decades, leading to this group of plants being listed in the second round of WoNS. In spite of these continuing challenges, the prickly pear management programme has left behind a successful legacy for the implementa-

tion of biological control for invasive plant species management in Australia. Research and management programmes for other such non-WoNS *Opuntia* species have been initiated due to the significant challenges posed by these species and the need to combat such problems.

Management of invasive plants can take several forms, being species-led, site-led and pathways-led (Downey and Sheppard 2006; McGeoch et al. 2016). The species-led approach 'adopted' in Australia differs significantly from that formally used in New Zealand in which species-led programmes are focused exclusively on the eradication of a newly established alien plant species (Owen 1998; Downey and Sheppard 2006). In addition to adopting a species-led approach through the WoNS programme, Australia has also adopted a pathways approach in the form of a quarantine and pre-border Weed Risk Assessment (WRA) system (Pheloung et al. 1999) to detect potentially invasive plants species deliberately imported into Australia. Australia initially adopted quarantine measures in 1908 that governed the importation of plant material, but many plant species were still deliberately introduced for crops, pastures and ornamental purposes during the twentieth century (see Hazard 1988; Lonsdale 1994; Cook and Dias 2006), despite widespread advertisement advising of the dangers of plant introductions from the middle of the century (i.e. the 1950s (see <https://collections.museumsvictoria.com.au/items/244998>)).

In 1965 a comprehensive Quarantine Weeds List was developed, which contained over 130 species, which encompassed potentially dangerous (weedy) species and collated prohibited weeds lists from all Australian states and territories. Within 10 years there were strong arguments to reduce the size of the list by developing a weed seed schedule as it was becoming 'unworkable' due to the associated costs to farmers (see Spurr 1976). In response to the growing concern of the invasive plant problem, the Australian Weed Committee proposed a standard scoring system to be used by the commonwealth, states and territories when assessing the 'weedy potential' of a species being imported into Australia, in order to

minimise the risk. The work of Hazard (1988) and the Australian Weeds Committee led to the development and adoption of a formal WRA system (Pheloung et al. 1999) to screen deliberate introductions.

Australia held the first international workshop on weed risk assessment in 1999 (see Groves et al. 2001) and a second workshop in 2007 (Downey et al. 2010b). Australia also played a significant role in the development of weed risk assessment approaches globally through both development of a pre-border WRA system (see Pheloung et al. 1999), which has been tested and applied in many countries, and a post-border Weed Risk Management system (see Downey et al. 2010b).

Further pathways-based management approaches have involved detailed assessments of specific 'importation' sectors (e.g. those resulting in the sale of ornamental plants or pasture species). For example, Groves et al. (2005) showed that 66% of naturalised and invasive plant species in Australia originated from the gardening sector, and Virtue et al. (2004) revealed that 94% of the 27,000 deliberate plant numbers imported into Australia were associated with the nursery trade. In another assessment of pathways, Lonsdale (1994) showed that 463 exotic grasses and legumes were imported into Australia for pasture improvement purposes of which 13% subsequently became invasive. Many of these species were supported by federally funded research programmes at the time (see Cook and Dias 2006). Such assessment of invasion pathways has been instrumental in the development of a national pre-border WRA system to limit the import of potentially invasive plant species.

Site-led management tends to be poorly defined and is generally not used formally in Australia, in contrast to the approach adopted in New Zealand (Downey and Sheppard 2006) which is based on the protection of specific conservation areas at threat from invasive plant species (Owen, 1998). In fact, site-led management of invasive plant species in Australia has taken on multiple forms, with actions for invasive plant management being included in most Plans of Management for protected areas and a range of

sites being identified in state and national plans for WoNS, based on the presence of biodiversity under threat. For example, the Bitou TAP identified approximately 350 sites containing 157 plant species and 24 ecological communities threatened by bitou bush, *C. monilifera* subsp. *rotundata*, in NSW (Downey 2010). Such plans that aim to abate the threat of invasive plants to native biodiversity encompass both a species- and site-led approach.

6.5 Future of Plant Invasions in Australia

In the seminal book 'Australian Weed Management Systems', Adkins and Walker (2000) outlined three key future challenges for managing plant invasions across Australia. These include (1) the problem of the 'dynamic and growing' alien plant flora, which includes the threat from alien plant species already present in Australia that have not yet reached their full potential distribution and abundance, as well as those introduced and not presently recorded as naturalised (i.e. many of the 27,000 species outlined by Virtue et al. (2004)) and those impacted by potential climatic changes (see further discussion below); (2) the need to develop and use environmentally and ecologically sustainable management approaches, driven in part by the increasing use of chemical weed management strategies and the growing issue of herbicide-resistant weed species; and (3) the integration and adoption of weed management approaches and research leading to successful on-the-ground outcomes. Additionally, there is a growing need to ensure that challenges associated with a lack of monitoring following weed management are addressed, as highlighted by Reid et al. (2009) during an evaluation of the 20 WoNS species.

To address the growing alien flora in Australia, particularly arising from the deliberate introduction of ornamental species, a recent initiative called the Plant Sure scheme has been established to enable growers, retail nurseries and purchasers of ornamental plants to grow, sell and buy non-native plants that are unlikely to escape and pose

a threat to the environment (see www.gardenin-responsibly.org.au). The Plant Sure scheme has been successfully trialled in NSW, and a second phase is being rolled out including an assessment tool to determine the likely invasiveness of a nominated species, a certification system for non-invasive species and education and awareness material.

A critical future challenge that remains is developing a better understanding of how invasive plants will respond to a rapidly changing Australian climate (Roger et al. 2015). To address this issue, assessments were initially carried out on individual invasive plant species (e.g. Siam weed (*Chromolaena odorata*)) (Kriticos et al. 2005) and examined the relationship between climate predictions based on native and alien ranges (Beaumont et al. 2009). However, given the number of naturalised plant species in Australia, a single species approach has not generally been practical or useful for managers and policymakers.

In response to this need, Roger et al. (2015) developed a process to assess large numbers of species in a dedicated searchable website for managers (www.weedfutures.net). This website currently has climate change predications for 2035 and 2065 for over 700 non-native naturalised and invasive plant species in Australia. The database behind this website has led to several key publications on the future challenges for alien plants species in Australia in terms of the next generation of invaders (Duursma et al. 2013) and invasion hotspots (O'Donnell et al. 2012) for alien plant species under climate change.

One additional challenge will be to gain an improved understanding of how invasive plants respond to chemical control under elevated levels of atmospheric CO₂. For example, Manea et al. (2011) examined the effects of herbicide on four C₄ exotic grass species in Australia under ambient and elevated CO₂ and found that three of these species showed increase herbicide resistance under an elevated CO₂ environment. Given that Adkins and Walker's (2000) second key challenge was herbicide resistance, which is a growing problem in Australia and elsewhere, any increased resistance due to elevated CO₂ could

require significant shifts in the management of alien plant species particularly with respect to the use of herbicides.

6.6 Conclusions

The separation of Australia from other land masses has resulted in the evolution of unique native flora and fauna. Colonisation over the past three centuries has resulted in the introduction of various invasive plants to Australia, placing significant selection pressure on their ability to successfully adapt to Australian climate conditions. Incursions of invasive plants have impacted both native vegetation and managed crops, endangering fragile ecosystems and already resource-strained agricultural systems. The management of invasive plants has required significant investment from local, state and federal government agencies, leading to the classification of most impactful invasive plants as Australian Weeds of National Significance (WoNS). Concerted efforts for management have also led to state and national strategies to control and ultimately eradicate some of these species. The coastal WoNS species *Chrysanthemoides monilifera* subsp. *rotundata*, for example, has been managed successfully through application of a combination of chemical, physical and biological control strategies. Similarly, the management of most invasive weeds has relied on the use of integrated management strategies, including biological controls, which provide robust control of those species over time. The case studies presented clearly suggest the importance of the study of the biology, physiology and chemistry of weed invaders to target effective control strategies for successful eradication.

Future Australian ecologists, weed scientists, land managers and agriculturalists will need to work together to address the continuing challenge of invasive plants under a changing climate. While Australia has had considerable success in managing the invasion of some key alien plant species of national importance (i.e. WoNS) and has also successfully eradicated several recently introduced species by focused management, the

success of invasive alien species management will clearly affect the current status of Australian biodiversity and our ability to preserve fragile native communities, maintain agricultural productivity and protect human health and well-being. Future investments in large-scale management of invasive plants will rely upon multidisciplinary interaction of scientists and landowners and regional, state and national coordination to deliver effective outcomes. We remain hopeful that federal investment in such coordinated efforts will be reinvigorated in coming years, as past programmes have proven highly effective in some cases and also introduced novel strategies for suppression and eradication of invasive plant species down under.

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European Plant Invasions

7

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Abstract

Using the Global Naturalized Alien Flora (GloNAF) database, this chapter describes the patterns in regional diversity of naturalized alien plants in Europe. GloNAF registered 4139 naturalized plant taxa, which makes Europe the second richest continent after North America, and represents an increase by 390 taxa (or 9.6%) compared to the inventory conducted during the 2000s by the DAISIE (Delivering Alien Invasive Species Inventories for Europe) project. Most naturalized species are recorded in England (1379), Sweden

(874), Scotland (861), Wales (835), France (716), the European part of Russia (649), Ukraine (626) and Norway (595), indicating that the northern part of the continent, in particular the British and Irish Isles and Scandinavia, is most heavily invaded. The rate of new introductions of plants that have become naturalized has increased sharply throughout the two past centuries and is not showing any signs of slowing down. Biogeographical, socio-economic and ecological factors drive the variation in regional naturalized species richness – high human population density and national wealth, cold

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temperate and Mediterranean zonobiomes, and habitats such as arable land, coastal habitats and ruderal sites are associated with high numbers of naturalized aliens. Europe has exchanged many species with other continents. The main donor of naturalized plants to Europe is temperate Asia (1265 more species received than donated); in contrast, Australasia and North America harbour many more naturalized species of European origin than they have supplied to Europe, 1159 and 1080, respectively. The 1926 naturalized aliens from other continents represent a 14.9% contribution to the total plant diversity in Europe. The most widespread naturalized species is *Erigeron canadensis*, native to North America, occurring in 47 regions (76%). Fifty-four plants appear on the list of invasive alien species based on impact classification, and four (*Acacia dealbata*, *Lantana camara*, *Pueraria lobata* and *Eichhornia crassipes*) are among the highest ranking species with potentially the most serious impacts.

Keywords

Alien plants · Distribution · Donor regions · Europe · Habitat · Historical dynamics · Naturalization · Origin · Plant invasions · Regional hotspots · Taxonomy · Temporal trends

7.1 Introduction

Europe, especially its Mediterranean region, has traditionally been considered a donor of invasive alien species to other parts of the world rather than a recipient. This is most likely for historical reasons and due to the long association of plants and animals in Europe with humans since the beginning of agriculture some 10,000 years ago (di Castri 1990). Recent research, however, has shown that the past decades may have changed this long-held pattern – plants and animals of alien origin now form a substantial part of the continent's biodiversity (DAISIE 2009; Hulme et al. 2009b; van Kleunen et al. 2015) and exert

large and diverse impacts on both the environment and the economy (Vilà et al. 2010; Kumschick et al. 2015; Rumlerová et al. 2016). Moreover, while Europe has been a net exporter of naturalized plants since the discovery of America (di Castri 1990), in the past 60 years, more naturalized plants are being imported to than exported from Europe (Seebens et al. 2015).

Although Europe has always been one of the most intensively researched continents from the perspective of plant invasions (Pyšek et al. 2008), until the mid-2000s, the information on the presence and distribution of alien plant species for most European countries was scattered in a variety of published and unpublished accounts and databases. Only few countries had sound information on the composition of their alien floras available in specialized checklists (e.g. Austria, Essl and Rabitsch 2002; the Czech Republic, Pyšek et al. 2002; Germany, Klotz et al. 2002; Ireland, Reynolds 2002; and the UK, Clement and Foster 1994; Preston et al. 2002, 2004). This situation has changed with the DAISIE (Delivering Alien Invasive Species Inventories for Europe) project which, for the first time, collated comprehensive data for the whole continent and dramatically improved the knowledge of the European alien flora (Lambdon et al. 2008; DAISIE 2009; Pyšek et al. 2009). The DAISIE database contained records of 3749 naturalized alien plant species (following the definition of Richardson et al. 2000) in Europe, of which 1780 were introduced to Europe from other continents, and the remaining were native in some parts of it and naturalized in others (Lambdon et al. 2008). Further knowledge on plant invasions in this continent came with the founding and development of the Global Naturalized Alien Flora (GloNAF) database. This resource contains information on the global distribution of naturalized alien plants in more than 1000 regions of the world and currently records ~14,000 taxa that are naturalized in at least one country, district, state or island (van Kleunen et al. 2019). For Europe, GloNAF updated, extended and standardized data from DAISIE so that our accumulated knowledge of Europe's naturalized flora is now enriched by global information on the distribution of natural-

ized alien plants (van Kleunen et al. 2015, 2019; Pyšek et al. 2017). The data in GloNAF are restricted to naturalized neophytes (i.e. species introduced after the year 1500; Holub and Jirásek 1967; Pyšek et al. 2004).

In this chapter, we use the data from GloNAF to describe the patterns in diversity and geographic distribution of naturalized plants in Europe and the taxonomic and life history structure of the European naturalized flora. This approach represents a major update of the previous detailed account, based on DAISIE, published more than a decade ago (Lambdon et al. 2008; Pyšek et al. 2009). Here we (i) highlight regions with the highest numbers of naturalized and invasive aliens and review factors underlying the variation in richness of regional alien floras, including the role of habitats, (ii) by focusing on the taxonomic composition of the naturalized alien flora of Europe, we identify the most successful species, genera and families, as well as the role played by species with different life histories, (iii) we also compare the situation in Europe with other continents and describe the rate of exchange with major donor regions of alien plants to Europe and vice versa, and (iv) finally, available data on impacts of invasive plants are summarized, and an overview of the currently most important legislation related to plant invasions is outlined.

7.2 Distribution of Naturalized and Invasive Alien Species Diversity Across European Regions

The analyses in this chapter are mainly based on the GloNAF database, which provided data across 81 European regions (e.g. countries, states, provinces, districts, islands). Version 1.1 of GloNAF registered 4139 naturalized alien plant taxa in Europe which makes this continent the second richest after Northern America, where 5958 naturalized taxa of alien origin are recorded (van Kleunen et al. 2015) – these figures include also taxa on the intraspecific levels; for simplicity they are further referred to as ‘species’. This rep-

resents an increase by 390 species (almost 10%) compared to the DAISIE inventory a decade ago (see Lambdon et al. 2008), yet the total number of naturalized alien plants in Europe is likely to be still higher. While most European countries are well covered, lack of data on naturalized floras for some regions in the European part of Russia currently results in rather low coverage for Europe as a whole in GloNAF (63.8% of the continent area; Pyšek et al. 2017). Work is currently under way to close this data gap (see, e.g. Vinogradova et al. 2018), and more species are likely to be identified as naturalized aliens in Europe.

The distribution of naturalized and invasive alien species (as defined by Richardson et al. 2000) richness in European regions is fairly uneven (Fig. 7.1). The highest numbers of naturalized species are recorded in the following countries or regions: England 1379, Sweden 874, Scotland 861, Wales 835, France 716, European part of Russia 649, Ukraine 626, Norway 595, Bulgaria 593, Belgium 508, Italy 478, Spain 454 and Germany 451. Some of these countries are on top also in terms of the percentage of naturalized species among the total flora, as a measure of the levels of invasion (sensu Chytrý et al. 2008) in some of the regions in the northern part of the continent, in particular in the British and Irish Isles and Scandinavia (England 47.0% of the total flora of the country, Wales 43.6%, Scotland 41.8%, European part of Russia 36.7%, Sweden 34.8%, Norway 32.2%, Denmark 29.1%, Ireland 28.3%). The relationship between the number of naturalized species and latitudinal location of the country, however, is not significant. At the global scale, north-western Europe is one of the global hotspots of naturalized alien species richness, alongside regions such as the western and eastern coasts of North America, South Africa, the south-eastern part of Australia, New Zealand, several Indian states and tropical Pacific Islands as well as individual islands across all oceans. In contrast, none of the global hotspots of invasive alien species (i.e. South Africa, India, California, Cuba, Florida, Queensland and Japan) are located in Europe (Pyšek et al. 2017).

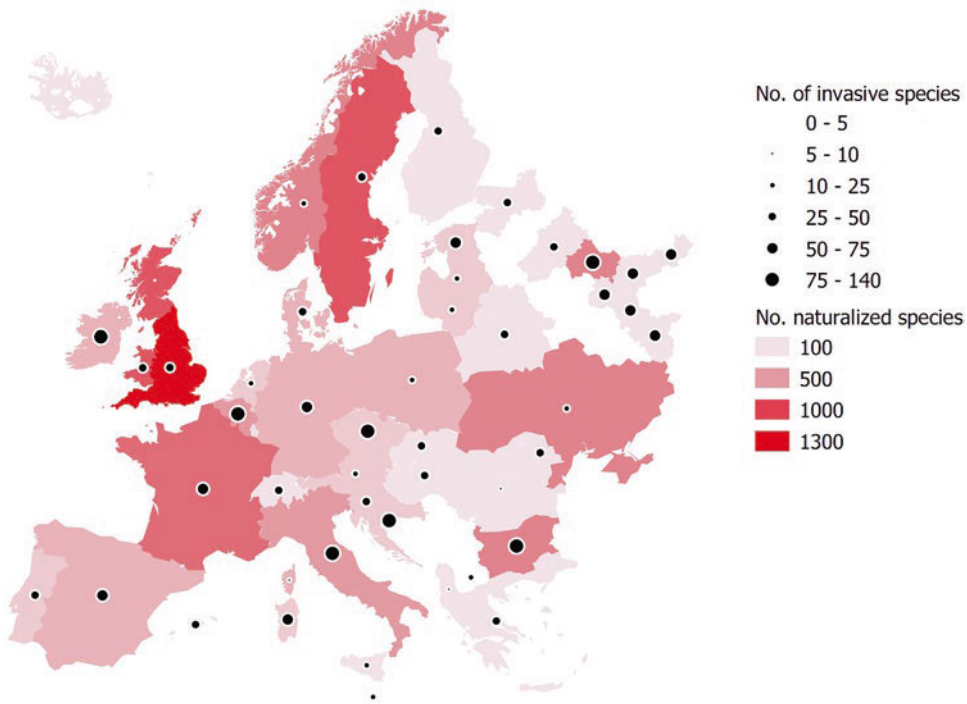


Fig. 7.1 The richness of naturalized and invasive alien plant species in European countries and regions. The numbers of naturalized species are shown by the shade of red and those of invasive alien species by the size of the black dot. Note that the colour scale is continuous and colours associated with the species numbers in the legend do not refer to discrete categories but to the thresholds of 100, 500, 1000 and 1300 species. The figure is based on data from Pyšek et al. (2017). Note that for European

countries whose floras distinguish two groups based on residence times, archaeophytes (alien species that arrived before the year 1492) and neophytes (species that arrived after the year 1492; Pyšek et al. 2004), only the latter were considered. This is because the archaeophyte status of some species is unclear, the classification is not available for all European regions, and the distinction is not being used in other regions of the world. White areas indicate missing data

Although the numbers of naturalized and native species per region tend to be positively correlated with each other, this correlation was significant neither for islands nor for mainland regions (Fig. 7.2a). This is different from the pattern observed at the global scale where the numbers of naturalized species on islands increased significantly faster with increasing native species richness than for mainland regions, and both relationships were highly significant (Pyšek et al. 2017). Overall, a positive relationship between alien and native species at this regional level is expected based on null models of community invasibility. These models predict the relationship to be negative at small spatial scales and positive at larger scales (Fridley et al. 2004),

when similar factors to those associated with the increase in native species with area, such as habitat heterogeneity, extensions of environmental gradients and increased probabilities of encountering disturbed habitats, are also responsible for establishment of more alien species (Stohlgren et al. 1999, 2003). Therefore, the lack of a significant correlation in the European data may indicate that some factors driving the richness of naturalized aliens differ from those determining the richness of native floras.

Those European mainland regions that are rich in naturalized aliens also harbour greater numbers of invasive alien species (Fig. 7.2b), but the relationship is only marginally significant ($p = 0.069$). It is interesting that for a given num-

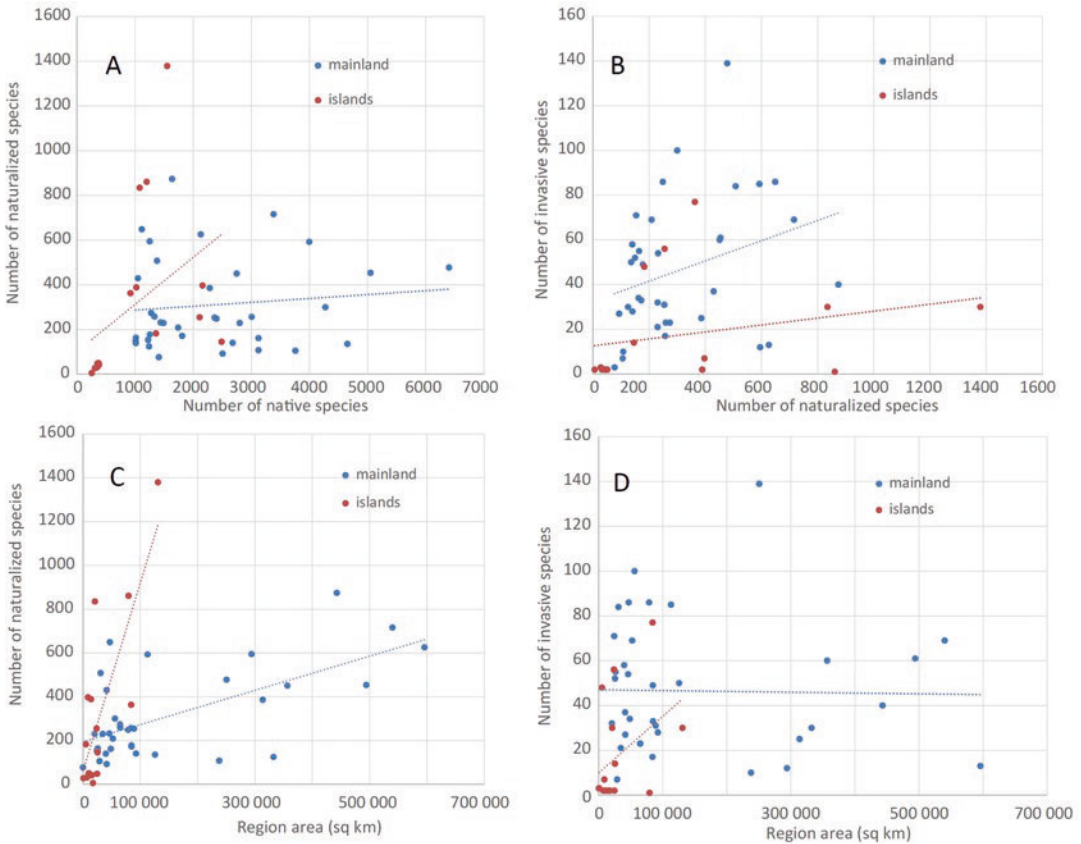


Fig. 7.2 Correlations of alien plant species numbers in European regions. (a) Number of naturalized species vs number of native species (mainland: $r = 0.11$, $t = 0.6593$, $df = 34$, $p = 0.514$, ns; islands: $r = 0.40$, $t = 1.6306$, $df = 14$, $p = 0.125$, ns). (b) Number of invasive alien species vs number of naturalized species (mainland: $r = 0.307$, $df = 34$, $p = 0.069$, ns; islands: $r = 0.26$, $t = 0.9863$, $df = 14$,

$p = 0.341$, ns). (c) Species-area relationship for naturalized species (mainland: $r = 0.63$, $t = 4.724$, $df = 34$, $p < 0.001$; islands: $r = 0.79$, $t = 4.855$, $df = 14$, $p < 0.001$) and (d) for invasive alien species (mainland: $r = -0.02$, $t = -0.1152$, $df = 34$, $p = 0.909$, ns; islands: $r = 0.38$, $t = 1.5436$, $df = 14$, $p = 0.145$, ns). The relationships are shown separately for mainland regions and islands. (Based on data in Pyšek et al. 2017)

ber of naturalized species, the number of invasive alien species is more than two times higher on the mainland than on islands (Fig. 7.2b). The species-area relationship for European regions is very steep for naturalized aliens on islands ($R^2 = 0.62$), but less so for mainland regions, where it still explains as much as 39% of variation (Fig. 7.2c). For invasive alien species, some increase with region area is only indicated on islands, but the relationship was non-significant (Fig. 7.2d). Although most of the relationships were not significant, the overall pattern is in line with the pattern observed for global alien floras (Pyšek et al. 2017).

7.3 Socio-Economic, Biogeographical and Ecological Factors Underlying the Variation in the Levels of Invasion in European Regions

Several studies analysing the determinants of naturalized species richness in Europe, including plants, have emphasized the importance of socio-economic drivers such as human population density and national wealth (Pyšek et al. 2010) and pointed to the phenomenon called invasion debt, i.e. that the consequences of the current economic

activities will only fully manifest in the future (Essl et al. 2011a; Seebens et al. 2015). For biogeographic and environmental factors, the high levels of invasions in Europe are in accordance with one of the important correlates of naturalized alien richness, the distribution of zoniomes. A global analysis of the effect of zoniomes on naturalized plant richness in mainland regions revealed that regions located in colder temperate and Mediterranean climates, i.e. the two most widely represented climates in Europe, harboured on average twice as many naturalized aliens (19%) as those located in arid temperate, subtropical and tropical climates (10%; Pyšek et al. 2017). In a study looking at Europe separately, Lambdon et al. (2008) found that the numbers of naturalized plants were determined mainly by the interaction of mean annual temperature and mean precipitation – they increased in regions with higher precipitation but only in warmer areas.

As to ecological determinants, studies that evaluated invasions in individual European habitats, based on thousands of vegetation plots (with sizes of units to hundreds of square meters), yielded consistent results about the representation of alien species in the most invaded habitats (Chytrý et al. 2008). Chytrý et al. (2005) found that the six most invaded habitats in the Czech Republic harboured on average 4.4–9.6% of neophytes (the average across all vegetation types was 2.3%). Vilà et al. (2007) found similar mean numbers of neophytes per plot in Catalonia (~2.0% pooled across habitats, and ~9.0% in the most invaded habitats). The highest proportions were reported from Great Britain, with maxima of 10–25% neophytes per plot in the three most invaded habitat types (Chytrý et al. 2008). The figures reported for archaeophytes (species introduced since the Neolithic until the end of the Medieval, i.e. before the year 1492; Pyšek et al. 2004) were much higher, with 56%, 36% and 22% on arable land, ruderal vegetation and trampled habitats in the Czech Republic, respectively, and 16% on arable land in Great Britain. These results can be generalized – habitats associated with human- and water-induced disturbances, high fertility and high propagule pressure exhibit

the highest levels of invasions. Pooled across regions, arable land, coastal sediments and ruderal habitats harbour the highest proportions of neophyte species in Europe (Pyšek et al. 2010). A regional study from the Czech Republic provides an evolutionary perspective on habitat invasibility, showing that alien species more strongly invade plant communities that are phylogenetically clustered, and because aliens tend to be related to native species, invaded communities become even more clustered (Lososová et al. 2015).

The data from the above studies of British, Catalanian and Czech habitats (Chytrý et al. 2008) were used to produce a European map of invasions by alien plants (Chytrý et al. 2009). This was done by translating habitat types to CORINE (Coordination of Information on the Environment) land cover classes (Moss and Wyatt 1994), which had been previously mapped across Europe from the interpretation of satellite images. The data from the three regions were extrapolated to other parts of Europe, using the framework of European biogeographical regions. The overall pattern indicates high levels of invasion in industrialized western Europe and in lowland agricultural regions in the east of the continent and lower levels of invasion in montane zones, oceanic areas in the north-west and the boreal zone (Chytrý et al. 2009). In a follow-up paper, Chytrý et al. (2012) projected the current levels of plant invasions in Europe under three different scenarios of economic development, based on changes in land use and climate (Spangenberg 2007) to project the future state of invasions by alien plants in Europe at three points of time (2020, 2050 and 2080). It revealed that invasions are likely to decrease in some areas and increase in others. Interestingly, the most environmentally friendly scenario, aiming at sustainability, will not result in the lowest levels of invasions. This is because this scenario was associated with the smallest increases in some regions, but also with the smallest decreases in invasions for other regions. The growth-oriented scenario would result in fewer invasions due to the more widespread abandonment of agricultural areas that are currently heavily invaded.

Overall, the polarization between more and less invaded regions is likely to increase if future policies are oriented toward economic deregulation, but an implementation of sustainability policies would not automatically restrict the spread of alien plants (Chytrý et al. 2012).

7.4 Sources of European Naturalized Flora and Exchange of Species With Other Continents

Besides 2213 naturalized species that resulted from introductions among regions within Europe (they are native to some part of the continent and naturalized in its other regions), there was an intense historical reciprocal exchange among Europe and other continents (defined by using the TDWG – Taxonomic Databases Working Group – biogeographical scheme; Brummit 2001), some of which were acting as major net donors of the European naturalized flora (Fig. 7.3). This was most pronounced for temperate Asia (1265 more species received than donated), with tropical Asia and Africa being the only two other continents that supplied more species to Europe than they received (277 and 161, respectively). All other continents harbour more naturalized species of European origin than they have supplied to Europe, the trend being most remarkable for Australasia (1159 more species donated) and Northern America (1080 species). Southern America has received 347 more species from Europe than it donated to Europe, and the corresponding figures for the Pacific Islands and Antarctica are 283 and 123 species, respectively.

These patterns of species exchange are reflected in the structure of the European naturalized flora by origin – European species are similarly frequent as species originating from temperate Asia (29.5% and 28.8% of all naturalized species with known area of origin, respectively), followed by Africa (15.0%, Northern America (10.1%), tropical Asia (8.5%) and Southern America (5.3%), with contributions from the Pacific Islands and Antarctica being negligible (Fig. 7.3). In addition, 35 taxa are of

hybrid origin and 109 are only known from cultivation.

Subtracting the 2213 species of European origin yields 1926 naturalized aliens that were introduced from other continents and have become a permanent component of the European flora. These species add to the 10,928 native plant species (Winter et al. 2009) and thus represent 14.9% of the total plant diversity in Europe, less than the 20.3% reported previously (Lambdon et al. 2008; Pyšek and Hulme 2011). The main reason for this discrepancy, besides data coverage that improved over time, is that the previous estimate was based on all alien species in the DAISIE database many of which were only casual (i.e. species that do not form self-replacing populations; sensu Richardson et al. 2000).

7.5 Historical Dynamics of Alien Plant Arrivals to Europe

Over the last 200 years, there has been a steady increase in the number of alien plant species arriving and subsequently naturalizing in Europe. In the nineteenth century, numerous plants were brought to Europe for ornamental purposes, as a result of plant-hunting expeditions and increased interest in ornamental horticulture (Fry 2013; Seebens et al. 2017; van Kleunen et al. 2018). Transport of living plants was facilitated by inventions such as the Wardian Case mobile greenhouse in 1829 (Fry 2013). At the global scale, and also in Europe, the first record rates of vascular plants remained high in the twentieth century (Fig. 7.4a), most likely as a consequence of the intensification of global trade (Seebens et al. 2015) and the increasingly widespread cultivation of plants in agriculture and botanic and private gardens (Hulme 2015; van Kleunen et al. 2018).

Lambdon et al. (2008) presented another insight into the dynamics of plant invasions in Europe, by using the minimum residence times calculated from the first record dates for 1883 naturalized neophyte species of which 954 were of European origin and 929 originated from other continents. When the cumulative number of alien

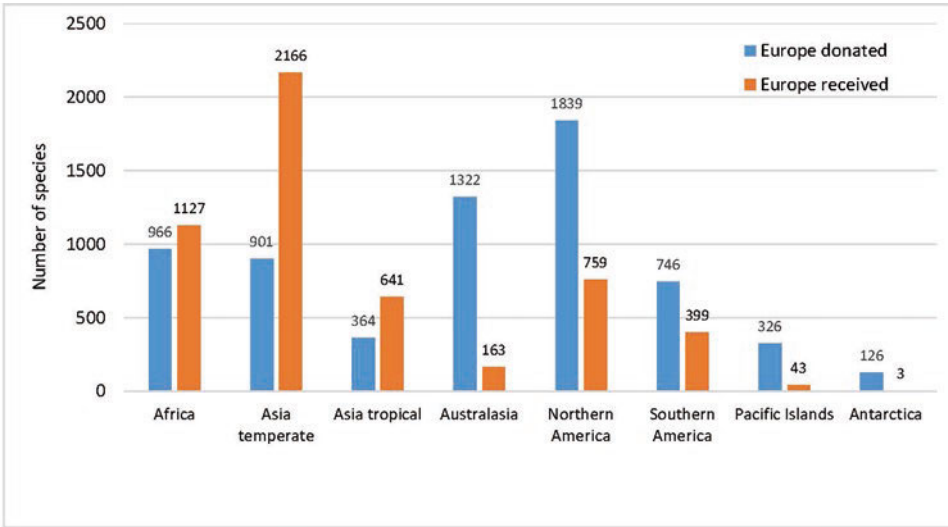


Fig. 7.3 Historical exchange of alien plant species among Europe and other continents (TDWG continents as recognized by the Biodiversity Information Standards Organization, originally Taxonomic Databases Working Group; Brummit 2001). The pairs of bars indicate the total number of native European species that have become nat-

uralized in a given continent (Europe donated) vs the number of species native to that continent that are recorded as naturalized in Europe. The differences in numbers of donated vs received species among continents are significant (G-test, df 7, $F = 354.9$, $p < 0.001$). (Based on data in van Kleunen et al. 2015)

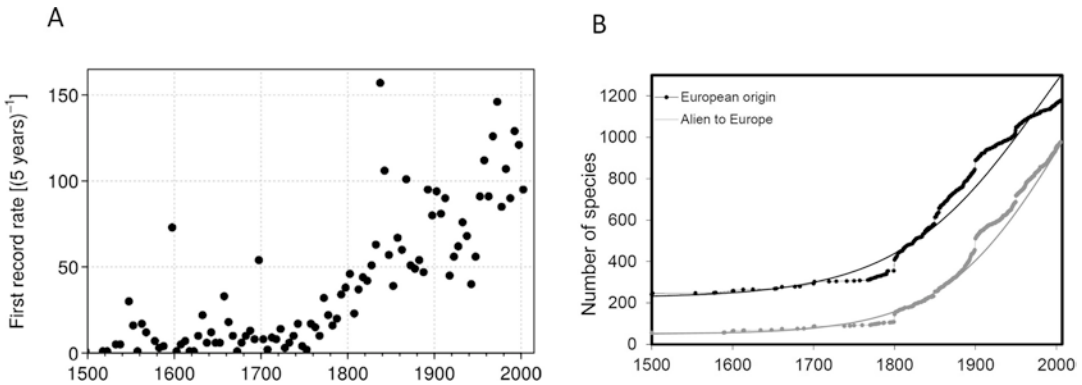


Fig. 7.4 Temporal trends in accumulation of alien plant species in Europe. (a) First records of alien species that have later become naturalized plotted for 5-year intervals. The plot is based on data from Seebens et al. (2017). (b) The number of species recorded as alien to at least one European country, in relation to their introduction date. Cumulative data are shown separately for species with

native distribution area outside of Europe: $T(p) = 0.0134y - 26.9$, $r^2 = 0.97$, $n = 929$; and those of European origin, but occurring as alien in other parts of the continent: $T(p) = 0.0113y - 22.40$, $r^2 = 0.95$, $n = 954$. (This plot was taken from Lambdon et al. (2008), with the permission of the Czech Botanical Society)

arrivals was plotted against time, there was a strongly exponential increase in the rate at which species capable of naturalization were being imported (Fig. 7.4b) – of the naturalized neophytes of non-European origin, 50% arrived after

1899, 25% arrived after 1962 and 10% arrived after 1989. Aliens of European origin tended to start their spread earlier, but the overall slope was very similar. The rate of new introductions has increased sharply throughout the past two centu-

ries and is showing little signs of slowing down (Lambdon et al. 2008).

Comparison of the current numbers of naturalized plants with the historical attempts to summarize European aliens can be used to estimate how quickly the naturalized flora of this continent has been increasing. In the first such study, Weber (1997) reported 1568 naturalized species in Europe, much less than recorded by DAISIE (2009) and recently by GloNAF (van Kleunen et al. 2015; Pyšek et al. 2017). The overview of Weber (1997) was based on the Flora Europaea, which relied on data from the 1960s to the 1970s (Tutin et al. 1964–1980), so one reason for the lower species number is simply time – since this period, there has been a continued influx of alien species to individual countries (Pyšek 2003). However, even then, many more alien species than included in that work must have been present in Europe. By taking into account residence times of naturalized species reported in the DAISIE database, Pyšek et al. (2009) estimated that there were 2175 naturalized aliens in Europe in 1980, when the publication of the first edition of Flora Europaea was completed, i.e. about 600 more than reported by Weber (1997).

7.6 The Most Widely Distributed Species

There are 35 species that have become naturalized in more than 30 regions, i.e. at least half of the European regions considered in the GloNAF database ($n = 62$, Table 7.1). The most widespread is *Erigeron canadensis*, occurring in 47 regions (i.e. 76% of the regions in Europe). Among the six most widely distributed naturalized species, there are another three in the Compositae family (*Matricaria matricarioides*, *Solidago canadensis*, *Galinsoga parviflora*), one representative each of the Hydrocharitaceae family (*Elodea canadensis*) and the Onagraceae family (*Oenothera biennis*). Among those 35 most successful naturalized species, the vast majority are perennial (15) and annual (14) herbs, with two additional shrubs (*Syringa vulgaris*, *Lycium*

barbarum), two trees (*Robinia pseudoacacia*, *Acer negundo*), one aquatic (*Elodea canadensis*) and one biennial herb (*Oenothera biennis*). Almost all of the most widespread naturalized aliens are native to Northern America (20 species) or temperate Asia (15), with only two having their region of origin partly in Europe (*Syringa vulgaris*, *Hesperis matronalis*) and five in Southern America (Table 7.1). So, the most widespread invaders in Europe originate in the Northern Hemisphere.

Surprisingly, being widespread as a naturalized alien in Europe does not translate into a wide global distribution as naturalized (Fig. 7.5). There is no significant correlation between the number of regions a species occupies in Europe and the rest of the world (Pearson product-moment correlation, $t = 1.1897$, $df = 33$, $p = 0.2426$). Figure 7.5 highlights examples of species that are widespread everywhere (*Erigeron canadensis*), common globally but less frequent in Europe (*Datura stramonium*, *Medicago sativa*) or widely distributed only in Europe (*Elodea canadensis*, *Oenothera biennis*). A special group are species that are serious invaders wherever they occur, but their distribution is relatively restricted both in Europe and all over the world (*Heracleum mantegazzianum*, *Fallopia* sp. div.).

The ranking of the most widely distributed naturalized aliens made by Lambdon et al. (2008), also based on the number of regions occupied, allows for a rough indication of changes in distributions during the last decade. Bearing in mind that the delimitation of regions in the current GloNAF-based analysis is more detailed, yielding a higher number of regions (62 vs 49), there is a significant correlation between both periods (Pearson's product-moment correlation: $t = 4.121$, $df = 33$, $p < 0.001$), nevertheless with some remarkable outliers. For example, *Elodea canadensis*, *Matricaria matricarioides* and *Oxalis stricta* seem to have gained in distribution compared to other species, whereas *Robinia pseudoacacia* that ranked second in 2008 is an example of the opposite trend (Table 7.1).

Table 7.1 The most widespread naturalized alien plant species in Europe, ranked according to the number of regions in which they are recorded as naturalized (column Europe, n = 62)

Rank	Taxon	Family	Life history	Origin	Europe	RegTot	Rank 2008
1	<i>Erigeron canadensis</i>	Compositae	Annual	N Am, S Am	47	234	1
2	<i>Elodea canadensis</i>	Hydrocharitaceae	Aquatic	N Am	46	75	13
3	<i>Matricaria matricarioides</i>	Compositae	Annual	As-temp	45	109	23
4	<i>Oenothera biennis</i>	Onagraceae	Biennial	As-temp	45	97	6
5	<i>Solidago canadensis</i>	Compositae	Perennial	N Am	44	119	7
6	<i>Galinsoga parviflora</i>	Compositae	Annual	N Am, S Am	43	216	8
7	<i>Amaranthus retroflexus</i>	Amaranthaceae	Annual	N Am	41	193	3
8	<i>Reynoutria japonica</i>	Polygonaceae	Perennial	As-temp	41	98	5
9	<i>Veronica persica</i>	Plantaginaceae	Annual	As-temp	40	183	9
10	<i>Helianthus tuberosus</i>	Compositae	Perennial	N Am	40	140	11
11	<i>Oxalis stricta</i>	Oxalidaceae	Perennial	N Am	40	52	30
12	<i>Robinia pseudoacacia</i>	Leguminosae	Tree	N Am	39	154	2
13	<i>Galinsoga quadriradiata</i>	Compositae	Annual	N Am	39	145	16
14	<i>Impatiens glandulifera</i>	Balsaminaceae	Annual	As-temp	39	74	17
15	<i>Juncus tenuis</i>	Juncaceae	Perennial	N Am, S Am	39	69	14
16	<i>Epilobium ciliatum</i>	Onagraceae	Perennial	As-temp, N Am, S Am	39	67	34
17	<i>Erigeron annuus</i>	Compositae	Annual	N Am	38	69	10
18	<i>Solidago gigantea</i>	Compositae	Perennial	N Am	38	43	18
19	<i>Impatiens parviflora</i>	Balsaminaceae	Annual	As-temp	37	45	19
20	<i>Bidens frondosa</i>	Compositae	Annual	N Am	36	44	22
21	<i>Amaranthus albus</i>	Amaranthaceae	Annual	N Am	35	129	20
22	<i>Syringa vulgaris</i>	Oleaceae	Shrub	Eur, A-temp	33	83	54
23	<i>Acer negundo</i>	Sapindaceae	Tree	N Am	33	82	12
24	<i>Symphotrichum novi-belgii</i>	Compositae	Perennial	N Am	33	58	40
25	<i>Heraclium mantegazzianum</i>	Apiaceae	Perennial	As-temp	33	53	41
26	<i>Datura stramonium</i>	Solanaceae	Annual	N Am	32	272	15
27	<i>Hesperis matronalis</i>	Brassicaceae	Perennial	Eur, As-temp	32	97	94
28	<i>Reynoutria sachalinensis</i>	Polygonaceae	Perennial	As-temp	32	71	27
29	<i>Bunias orientalis</i>	Brassicaceae	Perennial	As-temp	32	53	56
30	<i>Medicago sativa</i>	Leguminosae	Perennial	As-temp	31	242	24
31	<i>Cuscuta campestris</i>	Convolvulaceae	Annual	N Am, S Am	31	116	37
32	<i>Lycium barbarum</i>	Solanaceae	Shrub	As-tem	31	105	26
33	<i>Amaranthus blitoides</i>	Amaranthaceae	Annual	N Am	31	87	21
34	<i>Lupinus polyphyllus</i>	Leguminosae	Perennial	N Am	31	63	48
35	<i>Veronica filiformis</i>	Plantaginaceae	Perennial	As-temp	31	50	31

Species naturalized in at least half of the regions (31) are shown with information on their life history and native range (N Am, Northern America; S Am, Southern America; As-temp, temperate Asia; Eur, Europe). RegTot, total number of regions where the species has naturalized globally. Based on data from GloNAF database (van Kleunen et al. 2015, 2019; Pyšek et al. 2017). Rank 2008 – species' rank according to the number of regions from which it has been reported as naturalized in 2008, based on data from Lambdon et al. (2008)

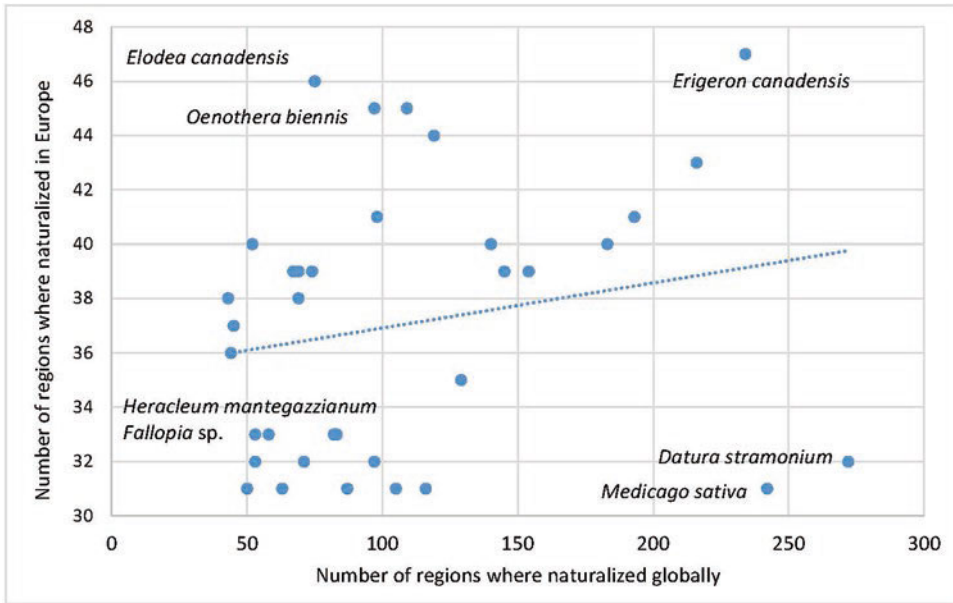


Fig. 7.5 The most widely distributed naturalized plant species in Europe in relation to their global distribution as naturalized. (Based on data from GloNAF. Pyšek et al. 2017; see Table 7.1)

7.7 Taxonomic and Life History Structure of the Naturalized Alien Flora of Europe

The following genera are most represented, measured by the number of naturalized species in Europe: *Cotoneaster* (73 species), *Oenothera* (55), *Euphorbia* (42), *Geranium* (35), *Salix* (33), *Sedum*, *Solanum* (both 31), *Rosa*, *Silene*, *Trifolium* (29), *Artemisia* (28), *Rumex*, *Allium* (27), *Narcissus*, *Crataegus* (26), *Rubus*, *Vicia* (25), *Prunus*, *Veronica*, *Bromus* (24), *Amaranthus*, *Centaurea* (23), *Iris* (22), *Populus*, *Senecio*, *Chenopodium*, *Campanula* (21), *Mentha*, *Medicago* and *Cyperus* (20). A genus whose naturalized species are most widely distributed in Europe, measured as the sum of regions where all its representatives are naturalized, is *Amaranthus* (275 species × region records), followed by *Cotoneaster* (220), *Oenothera* (220) and *Euphorbia* (214).

Nine families have more than 100 naturalized representatives in Europe. Compositae with 483 species built up 11.7% of the whole naturalized alien flora; corresponding figures for Gramineae are 334 species (8.1%), Rosaceae 321 (7.8%),

Leguminosae 237 (5.7%), Brassicaceae 179 (4.3%), Lamiaceae 117 (2.8%), Caryophyllaceae 106 (2.6%), Apiaceae 104 (2.5%) and Amaranthaceae 103 species (2.5%). The first three families are also most widely distributed with 2440, 1413 and 1400 species × region records, respectively. Largely these patterns reflect that some of those families are among the largest families worldwide.

As to the life histories, the European naturalized flora is dominated by herbaceous perennials (36.2%), annuals (21.5%) and biennials (7.5%), followed by grasses (5.9%), climbers (3.3%), aquatic plants (0.9%), succulents (0.9%) and epiphytes (0.1%). Shrubs and trees contribute 15.5% and 8.2% to the total number of species, respectively.

7.8 Impacts of Alien Plant Species in Europe

Europe was the first continent producing a continental-wide inventory of the magnitude and variety of ecological and economic impacts of invasive alien species (Vilà et al. 2010). This

assessment concerned negative impacts of alien plants, vertebrates and invertebrates on ecosystem services in terrestrial, freshwater and marine environments and revealed that there were 326 plant species with documented ecological impacts and 315 with economic impacts in Europe, representing 5.6% and 5.4% of the total number of alien plants recorded (Vilà et al. 2010). However, the real numbers are likely higher because for the vast majority of alien plants in Europe, the impacts are still unknown (Pyšek and Hulme 2011).

The assessment of impacts was put on a more quantitative basis with the development of standardized scoring tools (Nentwig et al. 2010, 2016; Blackburn et al. 2014). Kumschick et al. (2015) used the semi-quantitative generic impact scoring system (GISS), which describes environmental and socio-economic impacts using six categories of each. Their assessment was based on 128 species that are naturalized in Europe. Plants had a moderate total impact across categories compared to other taxonomic groups (with mammals having the highest and fish the lowest impact scores), and their environmental impacts were on average higher than their socio-economic impacts. The categories where most naturalized plants are reported in the literature to have an impact were competition with native taxa (84 out of 128 species evaluated) and ecosystem functioning (59 species), and in these two categories, the scores averaged across species were highest, indicating the strongest impacts. Compared to other groups, the impacts of alien plants in Europe are very broad, together with mammals; plants were the only taxon to exert impact on all 12 categories (see Kumschick et al. 2015; Nentwig et al. 2016 for details of the GISS classification).

Nentwig et al. (2018) integrated several scoring systems classifying the impacts of European aliens and proposed a list of 149 alien species with highest impacts, on which plants were the most numerous group, represented by 54 taxa. Four plants were included among the highest ranking species with the most serious potential impacts: *Acacia dealbata*, *Lantana camara*,

Pueraria lobata and *Eichhornia crassipes* (Nentwig et al. 2018).

In another European-focused study, Winter et al. (2009) demonstrated the effects of alien plant invasions on the homogenization of European regional floras. Using data from 23 regions and considering both native species losses due to extinctions and additions to the flora by aliens in concert, these authors showed that plant invasions since the year 1500 exceeded extinctions and resulted in increased taxonomic alpha diversity (measured by species richness) but decreased phylogenetic alpha diversity within European regions and increased taxonomic and phylogenetic similarity among European regions (i.e. decreased beta diversity). This was so because extinct species were phylogenetically and taxonomically unique and typical of individual regions, and extinctions usually were not continent-wide and therefore led to differentiation, while many naturalized alien species were widespread, thereby contributing to homogenization. As a result, floras of many European regions now have more species, but have partly lost and will continue to lose their uniqueness (Winter et al. 2009). Moreover, the homogenization of European floras is increasing, as can be inferred from a comparison of these results with a study using older data on alien plants that found a greater dissimilarity (Winter et al. 2010).

7.9 Legislation

Although the rates of species introductions to Europe accelerated significantly during the second half of the twentieth century and still follow a steep curve at present (Hulme et al. 2009b), concerted efforts to understand biological invasions across the continent are relatively recent (Hulme et al. 2009a). The current knowledge base, nevertheless, provides an excellent foundation for integrated management action – Europe is nowadays a continent with the most comprehensive information on its alien biota particularly in terms of distribution patterns, invasion history and impacts. Even though

Europe is not the world leader in biosecurity policy, which is most developed on islands such as New Zealand (Hulme 2011), significant progress has been made during the last decade in implementation of research recommendations into policy. The single most important achievement was the implementation of EU Regulation No. 1143/2014 of the European Parliament and the EU Council from 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species. This instrument aims at regulating invasive alien species in Europe using evidence-based risk assessment protocols and based on the cooperation between researchers and policymakers (Genovesi et al. 2014). The crucial component of the legislation is the list of invasive alien species of Union concern; after several updates there are now 66 species listed (https://ec.europa.eu/environment/nature/invasivealien/list/index_en.htm; as of 21 March 2021). Besides the EU legislation, there are national activities aimed at developing lists of aliens for management with varying legislative support (e.g. Essl et al. 2011b; Pergl et al. 2016; Sandvik et al. 2019). So, while Europe is still running behind with legislation on alien organisms, the first steps have been taken.

7.10 Conclusions

In this chapter, we summarize the most up-to-date information on the patterns in diversity and geographic distribution of naturalized plants in Europe and the taxonomic and life history structure of the European naturalized flora. This data, as accumulated during the last 2 years in a broad international cooperation in this continent, represents a solid basis for continuing scientific exploration of the mechanisms of plant invasions at the continental scale under ongoing global change, as well as for conservation efforts, management, policy and decision-making process.

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Plant Invasions in North America

8

Laura Weber Ploughe and Jeffrey S. Dukes

Abstract

North America has accumulated more naturalized species, or “alien species that form self-sustaining populations in new regions,” than any other continent (5958; 3513 of which come from outside the continent). Over the last 35 years, North America has seen a rapid increase in the number of plant invasions; species have arrived through the horticulture and aquarium trades, as agricultural contaminants, and via other accidental and intentional pathways. Introduced populations have persisted and expanded on the continent with the help of extensive land use change and growing transportation networks. The main driving forces of naturalization in North America have been found to be habitat legacy (i.e., the habit affinities of a plant species in their native range), propagule pressure, and residence time, which are modulated by specific biological traits (e.g., flowering periods, vigorous clonal growth, and tall stature) interacting differently with these drivers. Within North America,

more invasive plant species are found in cold temperate and Mediterranean climate zones than in arid, temperate arid, subtropical, and tropical climates. Economic activity (measured as per capita gross domestic product; GDP) also heavily influences the distribution of non-native species; areas with higher per capita GDP (~17,000 USD) have over twice the number of non-native plant species compared to regions with lower GDP. Currently, in the United States alone, over \$100 billion per year is spent on losses, damages, and the control of invasive species, with the bulk of those funds going toward weed control for crops, pastures, and forests. In addition to being a drain on the economy, invasive non-native plants disrupt ecosystems and can often have negative effects on ecosystem services, including altered hydrological and fire regimes, impacts on native species, and changes in soil properties and nutrient cycling. National legislation and international agreements have been implemented in attempts to reduce threats from non-native species to biodiversity, the economy, and human well-being.

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Alien species · Climate zone · Global trade ·
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species · Plant introductions

8.1 Introduction

This chapter focuses on plant invasions in North America and includes research from the United States (excluding territories), Mexico, and Canada. The aims for this chapter are to (1) describe the recorded history of biological invasions; (2) discuss the introduction pathways for non-native species into North America, including the roles of trade, transport, agriculture, horticulture, and disturbance on these introductions; (3) explore the plant traits and life histories that increase invasion success of non-native plants in North America; (4) describe the climate zones that are most heavily invaded by non-native plants; (5) examine the impacts that invasive plants have on ecosystem services, including impacts on hydrological and fire regimes, native species, soil properties, and nutrient cycling; and (6) discuss some of the national and international policy and legislation that has been enacted to control the spread of invasive plants in North America

8.1.1 A History of Biological Invasions in North America

North America's history of biological invasions can be divided into three periods. The first phase of modern biological invasions began around the year 1500 with the advent of global exploration, specifically the European rediscovery of the Americas, the birth of colonialism, and changes to agricultural trade and industry (Hewitt et al. 2009; Hulme 2009). By 1800 AD, the industrial revolution had begun, and along with it the second major phase of biological invasions in North America (Mack 2003; Hulme 2009). This period was defined by an exponential increase in global trade as well as a steady increase in the annual rate of plant introductions (Mack 2003; Hulme 2009). During this period, there were increases in international trade through new transportation routes and technologies, including canals, highways, railways, and steamships, and increases in emigration; over 50 million Europeans arrived in the United States between 1820 and 1930. This

increase in international activity provided avenues for the introduction of non-native plants (McNeely 2006; Findlay and O'Rourke 2007; Hulme 2009). Over the last 35 years, North America has seen a rapid increase in the number of plant invasions, suggesting a "step change" in biological invasions, bringing us into the third and current phase, the Era of Globalization (Hulme 2009). Recently, Seebens et al. (2017) showed that this increase in the number of non-native species shows no sign of saturation at the global scale. North America has accumulated more naturalized species than other areas of the world (van Kleunen et al. 2015; Pyšek et al. 2017; Seebens et al. 2021); these species are distributed unevenly across countries and their respective states or provinces (Fig. 8.1).

8.1.2 The Introduction of Non-native Species into North America

Non-native species have made their way into North America through a variety of pathways, including as stowaways on trade and transportation routes, and intentionally or unintentionally through agriculture, horticulture, and the aquarium trade. Land use change and disturbance have altered the receptivity of the landscape to invasions. Interestingly, we now know through advances in genetic technology and the tracing of genealogies of invasive plants that many species became invasive only after multiple introductions (Oduor et al. 2015). For example, chloroplast DNA sequences showed that black mustard (*Brassica nigra*) arrived in North America from multiple sources in its native range (Oduor et al. 2015).

Trade and Transport

Global trade and travel are primary drivers of the spread of invasive plants, and the step increase in invasive species recorded in recent decades could be linked to faster transportation routes, e.g., semi-trucks, trains, etc. (Meyerson and Mooney 2007; Hulme 2009; Seebens et al. 2015, 2017). International trade and travel are the primary

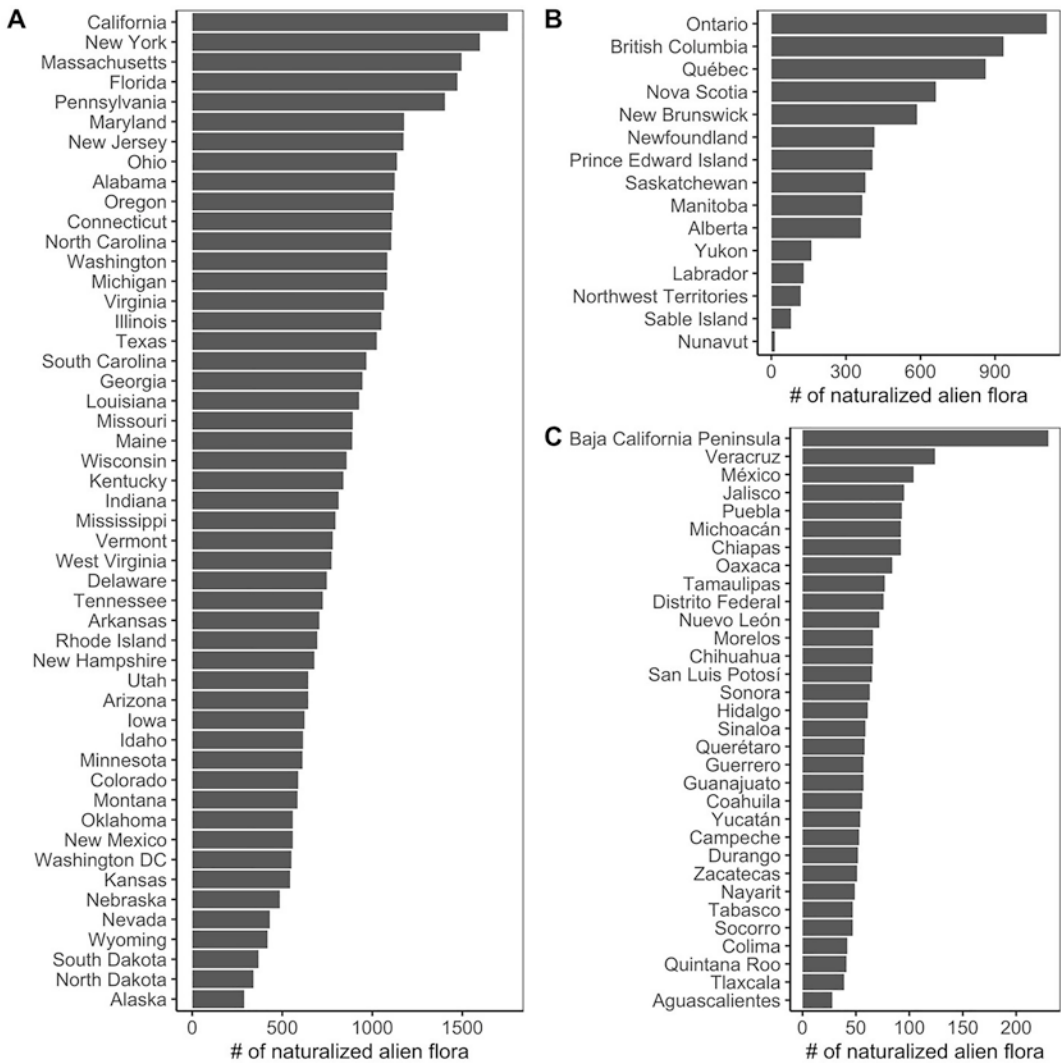


Fig. 8.1 Number of naturalized species per state or province for each North American country. Data was obtained from Global Naturalized Alien Flora (GloNAF) database

(van Kleunen et al. 2019; GloNAF; <https://gloناف.org/>). (a) United States of America; (b) Canada; (c) Mexico

sources of non-native plant stowaways or seed contaminants in goods and packaging material arriving by means of passenger planes and marine shipping ports (Hulme 2009; Tatem 2009; Levine and D’Antonio 2015; Bellard et al. 2016; Early et al. 2016). Generally, regions that have higher seaport and airport capacity and greater total imports are considered to be at greater risk of being invaded by a non-native species (Fig. 8.2; Early et al. 2016).

International air travel is playing an increasingly significant role in driving increases in the rates of biological introductions globally (Tatem 2009). Global airline traffic connects regions of similar climates. Climatic similarity with the native region is one of the requirements for establishment of non-native species (Bellard et al. 2016), along with propagule pressure and suitability of other abiotic factors (Hulme 2009). Thus, increases in travel and local climatic

changes could further increase the risk of the movement of non-native species and establishment in new areas (Ismail et al. 1999; Tatem 2009; Bellard et al. 2016). As illustrated in Fig. 8.2b, spatial patterns of air travel and importation of goods could affect the areas under threat from invasive species in the future (Early et al. 2016). In North America, the area that appears to have the greatest implied threat of invasive species arrival is the eastern portion of the United States.

Seaports have been a classic symbol for trade and economic development for centuries, but they are also gateways for introducing non-native species (Bellard et al. 2016). One means of introduction of non-native species in marine environments caused by shipping movements is the discharge of ballast material (Seebens et al. 2015; Bellard et al. 2016). In order for ships to remain balanced as they load and unload goods, the bottom of the ship is filled with ballast, any solid or liquid that is brought on the vessel to maintain stability. In the past, solid materials such as sand, rocks, and soils were commonly used and were often left behind at different destinations. This dry ballast was sometimes (if not frequently) contaminated with non-native plant seeds, resulting in new introductions (Mack 2003; Parks et al. 2005). One of the first studies exploring the possibility of alien plant species within dry ballast material found that of the 213 species identified, 93 species (~43%) were considered alien to the area investigated in Oregon, USA (Nelson 1917). As a result of these large

number of alien species, this practice becomes obsolete, but now ships use seawater for ballast, transferring a significant amount of ballast water between different continents and oceans (Government of Canada 2010; Werschkun et al. 2014).

Agriculture, Horticulture, and the Aquarium Trade

Many non-native species have been introduced to North America as seed contaminants in agriculture, through the cut flower trade, through the aquarium trade, or through forestry and horticulture. Many non-native agricultural weeds have been accidentally introduced as contaminants in crop seeds, despite the Federal Seed Act (FSA) in the United States (Ismail et al. 1999). FSA regulates the interstate and foreign transport of agricultural and vegetable seeds, requiring labeling and purity standards in commerce (US FSA 7th Cong. 1551–1611 (1988)). Cut flowers can also have seed contaminants within the flowers, which can be transported to new regions when airplane passengers carry bunches of flowers from one country to another (Ismail et al. 1999). The majority of plants used in agriculture, forestry, and horticulture in North America are non-native (Reichard and White 2001), and while most of these plants do not become invasive, a small proportion of species has escaped cultivation, established self-sustaining natural populations without human intervention, and become invasive (Reichard and White 2001; van Kleunen et al. 2018). For instance, St. John's wort (*Hypericum*

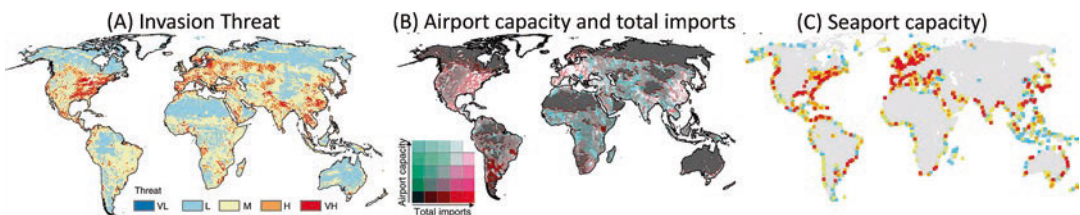


Fig. 8.2 (a) Invasion threat to North America for the twenty-first century. Colors indicate the level of invasion threat, from very high to low. The scale was determined by ranking the threat values of each of the map grid cells. The cells were then binned into percentiles: 100–90%, very high (VH); 90–80%, high (H); 80–50%, medium

(M); 50–20%, low (L); and 20–0%, very low (VL). (b) The impact of the combination of airport capacity and total imports on invasion threat. (c) Seaport capacity, an indicator of invasion threat from shipping. Colors are the same as indicated in Fig. 8.2a. All panels excerpted from Early et al. (2016)

perforatum) was introduced in the late 1700s as an ornamental for medicinal purposes in the eastern United States and was later found in the western United States in the mid-1800s (Campbell and Delfosse 1984; Reichard and White 2001; Mack 2003). *H. perforatum* is considered a noxious weed in both its native and non-native ranges and has harmful effects on livestock and both natural and agricultural lands (Mack 2003; Popay 2015). The species is now distributed throughout most states in the United States and in eastern provinces and British Columbia in Canada (Zouhar 2004); it is considered invasive in western North America (Popay 2015). Since its introduction, the abundance of *H. perforatum* has been effectively restrained in much of its new range through biological control (Mack 2003; Popay 2015).

The aquarium trade also presents a major risk for the introduction of aquatic non-native plants (Padilla and Williams 2004; Ricciardi et al. 2017; Della Venezia et al. 2018). In the United States, a major problem is that aquatic plants listed as federal or noxious weeds can nonetheless be purchased online, and most of the global trade likely takes place via this avenue. This creates difficulties for governments to enforce regulations, although US governmental agencies have been making headway in dealing with Internet trade (Padilla and Williams 2004). Water hyacinth (*Eichhornia crassipes*) is believed to have been introduced into Floridian waterways following the World's Industrial and Cotton Centennial Exposition in New Orleans in 1884, when it was brought home as a souvenir and released. *E. crassipes* has been nicknamed "the world's most troublesome weed" as a result of its ability to double in population size and create dense floating mats in about a week (Gopal and Sharma 1981; Padilla and Williams 2004). Since its introduction, Florida has appropriated millions of US dollars of state and federal funding to achieve limited control of *E. crassipes* (Padilla and Williams 2004). It is now found in several states, the province of Ontario in Canada, and in parts of Mexico.

While non-native plants are primarily introduced deliberately through the ornamental plant

trade (Reichard and White 2001; Mack and Erneberg 2002; Lehan et al. 2013), accidental introductions through seed contamination are of increasing concern as a major pathway for invasive plants (Lehan et al. 2013; Fig. 8.3). In the eastern United States, the majority of non-native angiosperms (64% of surveyed species) were introduced deliberately, whereas only 2% arrived accidentally as seed contaminants and the remainder of species had unknown origins (Mack and Erneberg 2002; Lehan et al. 2013). In the western United States, a high proportion of invasive plants – primarily grasses and forbs – arrived accidentally as seed contaminants, whereas in eastern states non-native plants primarily arrived through deliberate introduction as ornamentals (Lehan et al. 2013). In fact, although all types of invasive plants are more likely to be introduced deliberately, introduction pathways vary considerably by plant growth habit; a significantly larger percentage of forbs and grasses were accidentally introduced compared to vines, shrubs and trees. In the United States, accidental introductions account for at least 12% of all invasive plants and 21% of noxious weeds; these are likely underestimates because many species have unknown introduction pathways (Lehan et al. 2013). Seed contaminants account for the majority of accidental introductions in the United States (Lehan et al. 2013).

Land Use Change and Disturbance

As globalization increases, so does the amount of land use change and disturbance (Houghton and Nassikas 2017). In North America, the landscape is evolving to keep up with the demands of a rising population and global markets, as land is converted to support transportation routes, agricultural production, and energy infrastructure, among other things (Bradley et al. 2010; Houghton and Nassikas 2017). Disturbances to the land harm native plant populations and can provide opportunities for non-native species to benefit, for instance, by providing rapid large-scale increases in resource availability (Bradley et al. 2010). An example of this is deforestation, which increases light and belowground resource availability in a very short time frame. A strong

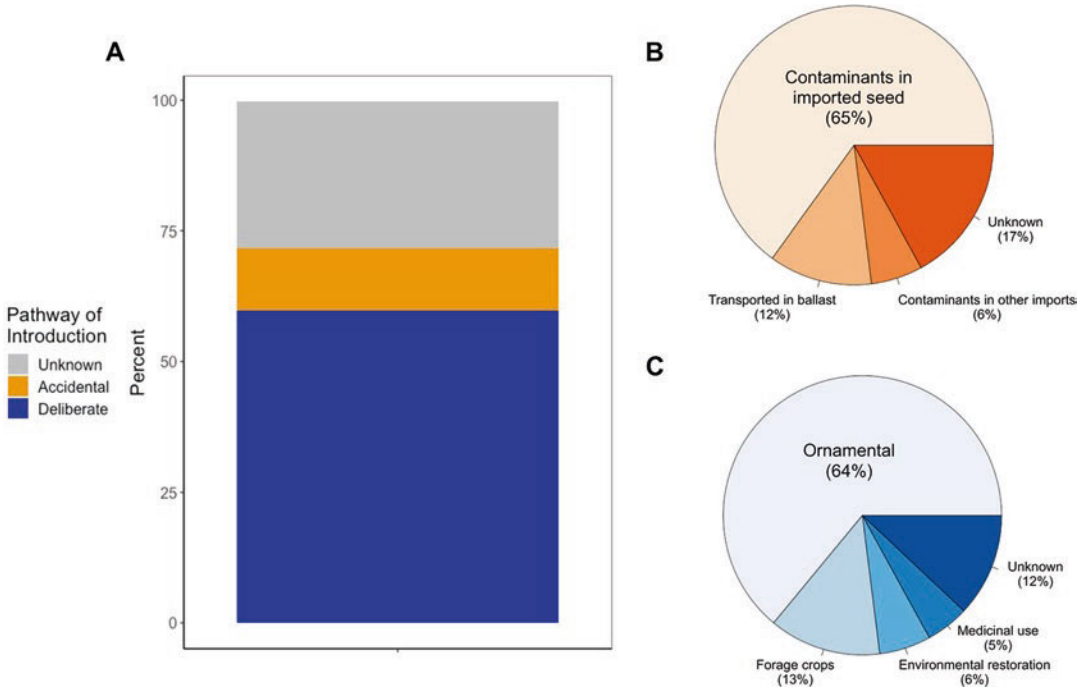


Fig. 8.3 Pathways for invasive plant introductions in the continental United States. (a) Deliberate, accidental, and unknown introduction pathways for invasive plants.

Specific introduction pathways for accidentally (b) and deliberately (c) introduced invasive plants. Data from Mack and Erneberg (2002) and Lehan et al. (2013)

positive relationship between physical disturbance and plant invasion has been found in several studies (as reviewed by Bradley et al. 2010). Disturbance types include roads (Larson 2002; Gelbard and Belnap 2003; Bradley and Mustard 2006), deforestation (Yates et al. 2004; Fan et al. 2013), urban areas (Turner et al. 2005; Pennington et al. 2010), energy development (Barney 2014; Villarreal et al. 2019), and agriculture (Pimentel 2009). The novelty, magnitude, and rate of disturbances often disadvantage native plants, causing the system to become less resistant to invasion (Bradley et al. 2010). Changes in disturbance regimes can allow for a different set of species, potentially invasive species, to persist and are therefore important for understanding invasive species establishment.

The intensity and global patterns of invasive plant establishment and disturbances are changing at a faster rate than any other period in recorded human history (Seebens et al. 2015; Early et al. 2016), indicating that the geographical patterns of future invasions will likely be very

different from today as land use change continues to expand (Foley et al. 2005; Theoharides and Dukes 2007; Early et al. 2016). In North America, many non-native species take advantage of such disturbances to become widely established and can subsequently suppress native species' populations (Bradley et al. 2010). In a study exploring the patterns of invasive plant diversity in Northwest mountain ecoregions, Parks et al. (2005) found that disturbed riparian systems and forests are especially vulnerable to plant invasion, whereas alpine and wilderness areas remain relatively unaffected by invasive plants. One such species that has been found to establish and thrive following a disturbance is pale swallow-wort (*Vincetoxicum rossicum*), a perennial, herbaceous vine native to southern Europe, which is of particular concern in the northeastern United States and southeastern Canada (Parks et al. 2005). It is expected that intense land use will likely continue to enhance invasive plant introductions into these low elevation mountain ecosystems (Parks et al. 2005).

8.2 Life History and Origin of Non-native Plants

Researchers often look to non-native plants' traits or life histories, including properties such as growth rate, nutrient use efficiency, stress tolerance, herbivore resistance, and reproduction strategy, to better understand why certain species become more invasive than others (Theoharides and Dukes 2007; Pyšek and Richardson 2008; Ricklefs et al. 2008; Pyšek et al. 2017). For example, Pyšek et al. (2015) used a model to identify plant traits that promote naturalization of central European species in North America and confirmed that traits such as longer flowering periods, vigorous clonal growth, and tall stature promoted invasion success in North America. Ultimately, the main driving force of naturalization has to do with a myriad of life history traits, and Pyšek (2015) demonstrated that habitat legacy, propagule pressure, and residence time are important driving forces in North America.

While Pyšek et al. (2015) specifically explored the naturalization of European species in North America, invasive plants from other regions tend to possess these same traits. For example, the Asian species Japanese knotweed (*Reynoutria japonica*) is a highly aggressive, invasive perennial in Europe and North America. The clonal species was introduced into the United Kingdom as a garden ornamental around 1830 and was reported as naturalized in the United States by 1894 (Merhoff et al. 2003; Grimsby et al. 2007). Clonal spread by rhizomes and rapid growth have been suggested as the major characteristics that make *R. japonica* difficult to control and a problematic invader (Grimsby et al. 2007). Interestingly, Grimsby et al. (2007) found evidence that *F. japonica* implements different reproductive strategies in Europe and North America. In the United Kingdom, *R. japonica* is a single female clone reproducing exclusively through vegetative growth or hybridization with other *Reynoutria* spp. (Bailey 1994; Hollingsworth and Bailey 2000; Grimsby et al. 2007). However, in the United States, Grimsby et al. (2007) found evidence of both asexual and sexual reproduction, resulting in populations of

knotweed that are genetically diverse, as these populations are not purely clonal. These complex reproductive dynamics of *Reynoutria* spp. and their widespread distribution indicate that the invasive potential of these species is far-reaching and is not fully realized (Grimsby et al. 2007). Further, this suggests that the invasion biology of *Reynoutria* spp. in the United States is different from that of knotweeds in Europe, demonstrating a need for regional studies of this likely rapidly evolving taxon in North America (Grimsby et al. 2007).

In addition to high genetic diversity, another trait that has been suggested to promote naturalization is a small genome size (Lavergne et al. 2010b; Pyšek et al. 2017, 2018). It has been theorized that small genomes allow species to have a shorter generation time and reproduce more quickly, leading to higher propagule pressure (Rejmanek and Richardson 1996; Pyšek et al. 2015). Comparative studies have shown that species with smaller genomes are more likely to become invasive than their relatives (Kubešová et al. 2010; Lavergne et al. 2010a, b; Pandit et al. 2014). Reed canary grass (*Phalaris arundinacea*), an invasive species in North America that is considered a major threat to native wetland vegetation and bird breeding habitat (Lavergne and Molofsky 2006; Lavergne et al. 2010b), has been used as a model to investigate whether reduced genome size could result in rapid phenotypic evolution (Lavergne et al. 2010b; Pyšek et al. 2018). It is suggested that the invasiveness of this species in North America was a result of multiple introductions and subsequent recombination of multiple European strains, allowing for rapid selection of novel genotypes with higher potential for vegetative reproduction (Lavergne and Molofsky 2004, 2007; Lavergne et al. 2010b). These novel genotypes of *P. arundinacea* in its invasive range have a smaller genome than European genotypes (Lavergne et al. 2010b), and this smaller genome size was associated with plant traits favoring invasiveness (long rhizomes, early emerging abundant shoots, resistance to aphid attack, and low C:N ratio; Pyšek et al. 2018).

8.3 Plant Invasions by Climate Zone

In North America, certain types of climate are more heavily invaded than others. In this section, we explore the number of invasive plant species that invaded each of North America's five most common climate zones: tropical (equatorial and savanna), subtropical (arid), Mediterranean, temperate (warm, arid, and cold/boreal), and Arctic (excerpted from the zoniomes outlined in Pyšek et al. (2017) and by Walter and Breckle (1991); Fig. 8.4a).

In North America, the colder temperate and Mediterranean climate zones harbor approximately twice the number of non-native plant species as regions with arid, temperate arid, subtropical and tropical climates (Pyšek et al. 2017). For example, forests in the eastern United States have been found to harbor more invasive species than those in the western regions of the country (Iannone et al. 2015; Oswalt et al. 2015; Fig. 8.4b). Per capita GDP heavily influences the distribution of non-native species in temperate arid, subtropical, and tropical regions. Areas with higher per capita GDP (~17,000 USD per capita) have over twice the percentage of non-native plant species in their floras (16%) compared to regions with lower GDP (6%). Table 8.1 contains a list of the most widely distributed naturalized species in North America according to climate zone (Pyšek et al. 2017). Note that these widely distributed species are not necessarily those thought to have the greatest ecological or economic impacts, or those of the greatest management concern.

8.4 Impacts on Ecosystem Processes and Services

Invasive non-native plants threaten ecosystems, habitats, and native species and are key drivers of human environmental change. Ecosystems provide a number of benefits, both ecological and economic, known as ecosystem services, e.g., provision of habitat, storage of carbon, and pollination (Fisher et al. 2009; IPBES 2018).

According to the most recent estimates, invasive species inflict over \$100 billion per year in associated losses, damages, and management expenses in the United States alone (Pimentel et al. 2005). In addition to being a drain on the economy, invasive non-native plants disrupt ecosystems (Dukes and Mooney 2004), altering ecosystem processes, and often have negative effects on ecosystem services (Charles and Dukes 2007). Invasive plants are abundant in all major habitats in North America, but their impacts on biodiversity, cultural values, and economics differ among subregions (IPBES 2018). Here, we discuss the impacts that invasive plants have on ecosystem services in North America.

8.4.1 Hydrological and Fire Regimes

Terrestrial ecosystems provide hydrological services that benefit people by providing freshwater supplies (Brauman et al. 2007) and flood control. Invasive plants can alter the hydrology of ecosystems by changing the rate and/or timing of evapotranspiration (ET) or runoff, as a consequence of differences in transpiration rates, phenology, growth, or rooting depth of non-native versus native species (Levine et al. 2003). Some invasive plant species, particularly trees, use more water than native species (Calder and Dye 2001). Hydrological studies investigating the effects of removing invasive woody species have shown reductions in ET (Cleverly et al. 2006), rises in the water table (Asbjornsen et al. 2007), and increased water yield (Dye and Jarman 2004). For example, a removal experiment in Hawaii exploring the effects of three invasive tree species, *Cecropia obtusifolia*, *Macaranga mappia*, and *Melastoma septemnerium*, on stands of the native tree species *Metrosideros polymorpha* found that stand-level water use within removal plots was half that of the invaded plots, despite a significant increase in compensatory water use by the native tree (Cavaleri et al. 2014). However, other experiments have shown the potential for increased stand ET after invasive woody plant removal as a result of compensatory water use by

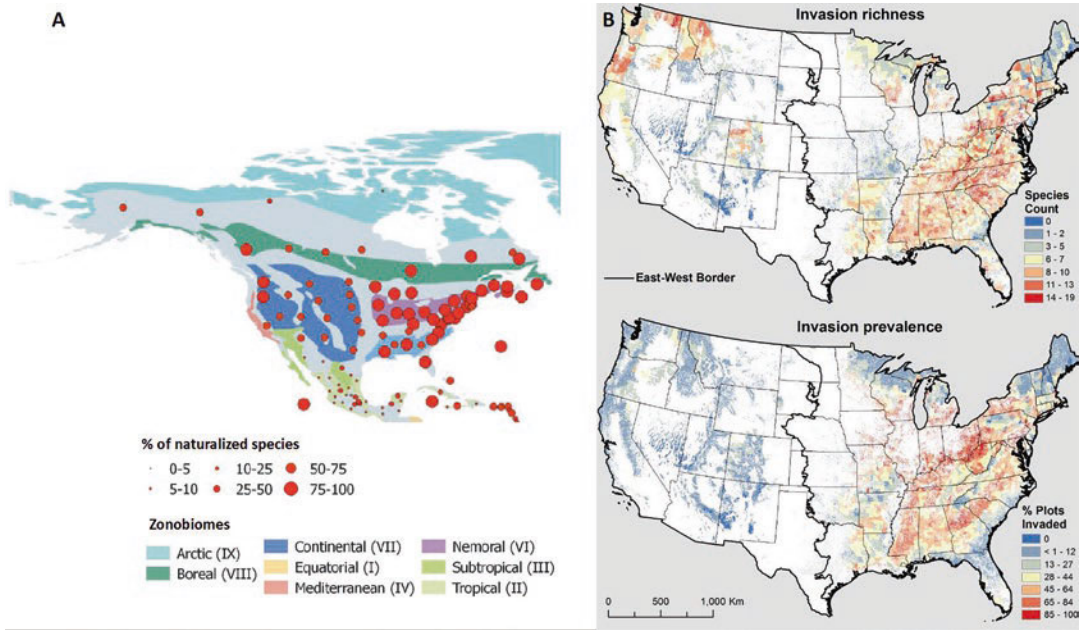


Fig. 8.4 (a) Naturalization in North America according to zonobiome. The red dots indicate naturalization hotspots based on the percentage of naturalized species within regional floras. Excerpted from Pyšek et al. 2017.

(b) Geographic patterns of forest plant invasion in the contiguous 48 states of the United States for (top) invasion richness and (bottom) invasion prevalence. Excerpted from Iannone et al. (2015)

Table 8.1 Common naturalized species of North America according to climate zones outlined in Walter and Breckle (1991) and excerpted from Pyšek et al. (2017)

Tropical and subtropical	Mediterranean	Temperate	Arctic
<i>Ricinus communis</i>	<i>Anagallis arvensis</i>	<i>Lolium perenne</i>	<i>Alopecurus pratensis</i>
<i>Sonchus oleraceus</i>	<i>Capsella bursa-pastoris</i>	<i>Chenopodium album</i>	<i>Dactylis glomerata</i>
<i>Bidens pilosa</i>	<i>Chenopodium album</i>	<i>Capsella bursa-pastoris</i>	<i>Phleum pratense</i>
<i>Eleusine indica</i>	<i>Medicago sativa</i>	<i>Stellaria media</i>	<i>Leucanthemum vulgare</i>
<i>Catharanthus roseus</i>	<i>Chenopodium murale</i>	<i>Brassica rapa</i>	<i>Matricaria matricarioides</i>
<i>Portulaca oleracea</i>	<i>Melilotus indicus</i>	<i>Datura stramonium</i>	<i>Poa annua</i>
<i>Chenopodium murale</i>	<i>Amaranthus hybridus</i>	<i>Echinochloa crus-galli</i>	<i>Trifolium pratense</i>
<i>Erodium cicutarium</i>	<i>Centaurea melitensis</i>	<i>Poa annua</i>	<i>Fallopia convolvulus</i>
<i>Medicago polymorpha</i>			<i>Lamium amplexicaule</i>
<i>Chenopodium album</i>			
<i>Marrubium vulgare</i>			

the remaining native species (Moore and Owens 2012) and little to no changes in water yield (Doody et al. 2011; Moore and Owens 2012). Alterations to the hydrology of the ecosystem as a result of invasion depend largely on the species involved and site-specific conditions (Dye and Jarman 2004; Doody et al. 2011; Cavaleri et al. 2014). Changes in hydrology are not only caused by invasion of woody plant species; some herba-

ceous invasive species have been shown to alter water cycling. For example, in annual grasslands in western North America, yellow starthistle (*Centaurea solstitialis*) has increased summer water use by 105–120 mm year⁻¹ (Gerlach 2001; Levine et al. 2003). Invasive annual grasses with shallow root systems, such as cheatgrass (*Bromus tectorum*), can change hydrology by competitively excluding deeper-rooted native perennials

(Dyer and Rice 1999; Bradley et al. 2018; Fusco et al. 2019).

While fires are natural events in many ecosystems, invasive species can alter fire regimes, and there are many examples of invaders increasing fire frequency. This is particularly true of invasions of grasses into otherwise woody species-dominant systems; some non-native grasses create a more continuous fuel bed that was not previously found in the invaded system (Levine et al. 2003; Fusco et al. 2019). *B. tectorum* in particular has been found to dramatically accelerate fire regimes in western North America (Brooks et al. 2006; Balch et al. 2013; Bradley et al. 2018). In a study exploring fire frequency in the Great Basin, United States, from 1980 to 2009, where *B. tectorum* dominates at least 6% of landscape, *B. tectorum* was found to burn nearly four times more frequently than any other type of native vegetation (Balch et al. 2013). Fires were more likely to ignite in cheatgrass than in other types of vegetation, and cheatgrass was associated with increased fire frequency, size, and duration, suggesting even small amounts of cheatgrass in an ecosystem can increase fire risk and alter fire regimes (Balch et al. 2013; Bradley et al. 2018). Most of the native shrub species cannot persist in locations where *B. tectorum* increases fire frequency (Whisenant 1990; Brooks et al. 2006). In addition to *B. tectorum*, Fusco et al. (2019) found evidence for significant alteration to regional fire regimes for seven additional invasive grass species in different ecoregions of the United States: *Taeniatherum caput-medusae* in the Great Basin, *Pennisetum ciliare* and *Schismus barbatus* in the desert southwest, *Microstegium vimineum* and *Miscanthus sinensis* in eastern temperate deciduous forests, and *Imperata cylindrica* and *Neyraudia reynaudiana* in southern pine savannah and pine rockland communities. These eight invasive grass species are associated with increases in rates of fire occurrence of 27–230% in the United States (Fusco et al. 2019).

In contrast, the invasion of stem-succulent plants can increase the moisture content of live fuels, making it more difficult for fires to ignite and spread (Brooks et al. 2006). The reduction of fires in some regions of North America reduces

the recruitment and growth of native shrub species (D'Antonio et al. 1993; Brooks et al. 2006). Invasion of the non-native succulent, hottentotfig (*Carpobrotus edulis*), has become a common event after a fire in the maritime chaparral in California, USA (Zedler and Scheid 1988). In this case, the invasion of *C. edulis* reduces fire frequency and can eventually lead to the conversion of maritime chaparral to a mix of succulent- and shrub-dominated vegetation (Brooks et al. 2006).

8.4.2 Consequences for the Displacement of Native Species by Non-native Plants

Invasive plant species displace and suppress populations of native plant species, which can have significant economic as well as ecological impacts on plant communities. For example, yellow starthistle (*Centaurea solstitialis*), which infests rangelands, is unpalatable to cows and toxic to horses and costs California \$7.65 million annually in livestock forage loss and ranchers an additional \$9.45 million in out-of-pocket expenditures (Eagle et al. 2007; Pejchar and Mooney 2009).

The impact of invasive species on agriculture is not just felt in terrestrial agriculture, but also in aquatic food production (Pejchar and Mooney 2009). Eurasian watermilfoil (*Myriophyllum spicatum*) is one of the most widely distributed non-native aquatic plants in North America; the weed is established in 48 states (except Hawaii and Wyoming) and in the Canadian Provinces of British Columbia, Ontario, and Quebec (U.S. Fish & Wildlife Service 2018). *Myriophyllum spicatum* has high environmental and socio-economic impacts as well as moderate beneficial impacts in the Great Lakes. The environmental impacts of *M. spicatum* included a potential reduction in the abundance and diversity of non-native insects and other benthic macroinvertebrates compared to native communities (Keast 1984), a reduction in the growth and vigor of warm-water fishery, and a reduction in nutritional value for waterfowl compared to native plants it replaces (Aiken et al.

1979). The species can alter the hydrology of waterbodies and create stagnant water conditions for parasites that cause swimmer's itch and promote mosquitoes (Jacobs and Margold 2009). Further, dense mats of *M. spicatum* can reduce water flow or clog agricultural, residential, or commercial water intakes, which can be expensive to unclog (Jacobs and Margold 2009; U.S. Fish and Wildlife Service 2018).

In addition to altering agroecosystems, invasive plants also have consequences for the biodiversity of native plant communities. Researchers often suggest strong competitive effects of invasive species on the growth, reproduction, and resource allocation of native residents as a mechanism for plant invasion (Levine et al. 2003). Dyer and Rice (1999) found that non-native annual vegetation changed seasonal patterns of resource availability in California's inland grasslands. Here, increased competition for light in the spring, when rapid growth of annuals tends to occur, suppresses the growth of native perennial bunchgrasses and reduces access to belowground resources through competitive inference. These changes in resource availability eventually result in the loss of perennial grasses, general dominance of non-native annual species, and a relative underutilization of deep soil resources. This example shows how phenology of non-native species and the seasonal shifts in resource availability as a result of their dominance can shift the primary limiting resource from soil moisture to light and alter the seasonal timing of resource limitation (Dyer and Rice 1999).

In addition to affecting biodiversity through competition and by changing disturbance regimes, non-native plant species have been found to affect native plant species by hybridizing with them. Hybridization can have evolutionary consequences; native species can be reduced or lost as native genes are diluted by invasive genes. Hybridization can play a role in the successful spread of invasive plants, hybrids, and their genes (Ellstrand and Schierenbeck 2000; Blair and Hufbauer 2010). Hybridizations can be interspecific or intraspecific, so it is possible that a hybridization event among well-differentiated populations within the same species may act in

the same way as hybridization among species and serve as a stimulus for the evolution of invasiveness (Ellstrand and Schierenbeck 2000). One intraspecific hybridization event(s) that increased invasiveness in North America took place in *B. tectorum*. *Bromus tectorum* in North America was found to have greater within-population genetic variation than populations in its native range, likely the result of hybridization of populations from multiple introductions (Novak and Mack 1993; Ellstrand and Schierenbeck 2000).

Invasive species with the ability to hybridize may benefit from evolutionary novelty and/or increased genetic variation. These properties may provide genetic material for rapid adaptation to abiotic and biotic conditions (Blair and Hufbauer 2010). *Typha* × *glauca* (*Typhaceae*) is a hybrid between *T. latifolia* (native) and *T. angustifolia* and is aggressive in disturbed wetlands in the eastern United States, such in the Great Lakes wetlands, especially when watersheds are urbanized (Zedler and Kercher 2004; Frieswyk and Zedler 2007). This species is sterile, but offspring spread aggressively through rhizomes that crowd out native species (Zedler and Kercher 2004). As mentioned previously, knotweed species (*Fallopia* spp.) hybridize in the United States but do not appear to have hybridized in their invasive range in Europe (Grimsby et al. 2007).

Hybridization among knapweed species (*Centaurea* spp.) makes these plants some of the most economically and ecologically detrimental introduced plants in western North America (Watson and Renney 1974; Blair and Hufbauer 2010). These species are capable of hybridizing with other knapweeds: *Centaurea* × *psammogena* is a hybrid between two non-native plants, spotted knapweed (*C. stoebe*) and diffuse knapweed (*C. diffusa*). Debate around *Centaurea* × *psammogena* has suggested that the plants are diffuse knapweed, expressing variable genotypes as a result of loose gene control (Watson and Renney 1974; Blair and Hufbauer 2010). More sophisticated genetic techniques have now made it possible to explore whether this hybridization in fact occurred. Blair and Hufbauer (2010) explored the hybridization of these two knapweeds at the molecular level and found hybrid-

ization had occurred in some individuals, but plants with intermediate morphology did not show evidence of mixed ancestry more often than plants with typical morphology of diffuse knapweed. Thus, in North America, sites that have both diffuse and spotted knapweed will likely include hybrid swarms (Blair and Hufbauer 2010).

8.4.3 Impacts on Soil Properties and Nutrient Cycling

Plants also modify the physical and chemical nature of the soil, altering biogeochemical processes and soil structure (Weidenhamer and Callaway 2010; Fei et al. 2014). Invasive plants primarily impact geomorphic properties of an ecosystem through bioprotection or bioconstruction (Fei et al. 2014). Bioprotection effects are properties that reduce or inhibit erosion or weathering, whereas bioconstruction refers to sedimentary accretion caused or facilitated by invasive species or through formation of organically dominated surface layers (e.g., leaf litter; Fei et al. 2014). Many invasive plants were originally introduced to novel ecosystems because they have geoprotective properties. A classic example in North America is the introduction of a vine native to Asia, kudzu (*Pueraria montana*), to the southeastern United States for erosion control. *Pueraria montana* forms a dense protective cover trapping sediments and infilling eroded gullies; however, since its introduction kudzu has overwhelmed the landscape in some areas, engulfing fields, trees, poles, and abandoned dwellings (Winberry and Jones 1973; Fei et al. 2014).

Similarly, European beachgrass (*Ammophila arenaria*) was introduced into San Francisco's Golden Gate Park from northern Europe around 1869 with the intention of stabilizing sand dunes (Lamb 1898; Schroeder et al. 1977; Dukes and Mooney 2004). *Ammophila arenaria* has since colonized dunes along much of the US Pacific coast (Dukes and Mooney 2004). This species is thought to have become invasive for several reasons: (1) multiple introductions and introduction sites, via widespread planting of *A. arenaria*

for 100 years after introduction (Wiedemann and Pickart 1996); (2) rapid within-site spread, through lateral growth of rhizomes; and (3) effective dispersal, as living rhizome fragments can wash down shore and colonize new locations (Wallén 1980). *Ammophila arenaria* collects sand more effectively than the previously dominant native dune grass *Leymus mollis* (Dukes and Mooney 2004; Barbour et al. 2007). This results in the development of steep, continuous foredunes, as high as 10 m, along the coast (Wiedemann and Pickart 1996). These large foredunes may inhibit active inland dune systems from collecting sand, resulting in more static systems that do not allow for establishment of native plants (Dukes and Mooney 2004).

In addition to bioprotective properties, non-native plants also impact geomorphology through bioconstruction by altering sediment deposition or litter accumulation rates (Dukes and Mooney 2004; Fei et al. 2014). In riparian ecosystems, salt cedar (*Tamarix* spp.) encroachment upon formerly unoccupied sandbanks along riverbanks has resulted in stabilization of sediments and slowed water velocity (Blackburn et al. 1982). As water movement is reduced, sediment deposition increases further and river channels narrow, increasing the flooding frequency of rivers (Blackburn et al. 1982). Like *Tamarix*, other freshwater invasive plants have been shown to increase sedimentation. Floating plants such as water hyacinth (*Eichhornia crassipes*) increase sedimentation through their complex root structure (Gopal 1987), and emergent plants such as papa grass (*Urochloa mutica*) and submerged plants such as water thyme (*Hydrilla verticillata*) increase sediment accumulation rates by reducing flow velocity and litter accumulation (Langeland 1996; Bunn et al. 1998). Other invasive plants can accelerate erosion (Dukes and Mooney 2004; Fei et al. 2014). For example, spotted knapweed (*Centaurea maculosa*) displaced native bunchgrasses throughout many rangelands of western North America (Tyser and Key 1988; Lindquist et al. 1996). The presence of *C. maculosa* results in greater losses of sediment and greater runoff from areas dominated by this

species than bunchgrass communities (Lacey et al. 1989).

Through these types of alterations to geomorphic properties, invasive plants can alter soil chemical and physical properties, influencing nutrient availability. Invasive species frequently have higher specific leaf area, growth rate, and leaf nutrient concentration compared to their native counterparts; these traits have the potential to accelerate decomposition and nutrient cycling (Allison and Vitousek 2004; Liao et al. 2008; Weidenhamer and Callaway 2010). For example, in deciduous forests in North America, areas invaded by garlic mustard (*Alliaria petiolata*), a biennial forb from Europe, have soils with significantly higher nutrient availability and soil pH (Reinhart and Callaway 2006; Rodgers et al. 2008). This may be the result of the significantly higher rates of leaf decomposition of this species compared to native trees (Reinhart and Callaway 2006; Rodgers et al. 2008). Higher nutrient contents in soils have also been found in western North America with the invasion of cheatgrass (*B. tectorum*; (Blank 2008) and the succulent, hottentot-fig (*Carpobrotus edulis* Renz and Blank 2004; Reinhart and Callaway 2006).

The examples above demonstrate the interwoven relationships of plants and soil biota known as plant-soil feedbacks (Reinhart and Callaway 2006). These feedbacks are considered positive when plant species increase beneficial soil biota, including mycorrhizal fungi, nitrogen-fixing bacteria, and other soil organisms that increase plant growth. Plant-soil feedbacks are considered negative when plants boost the abundance of soil-borne pathogens, herbivores, and parasites (Reinhart and Callaway 2006). In some invaded ecosystems, plant invaders promote soil biota that may even promote the establishment and invasion of non-native species, making plant-soil feedback processes an important component of invasion (Callaway et al. 2004). Rare species in North America consistently demonstrate negative feedbacks with soil microbes that promote biological diversity; conversely, abundant non-native and native species tend to produce positive feedbacks that can reduce biodiversity. Positive feedbacks occur when a plant species accumulates

microbes near their roots that have beneficial effects on the plants that harbor them, such as mycorrhizal fungi or bacterial nitrogen fixers, which can lead to a reduction in biodiversity. Negative feedbacks occur when plant species accumulate pathogenic microbes in their rhizospheres that create increasingly hostile conditions to the plants that cultivate these pathogens, resulting in increased species turnover rates and, therefore, greater diversity. For example, soil microbes obtained from European soils in the native range of spotted knapweed (*C. maculosa*) were found to have stronger inhibitory effects on that plant's growth than soil microbes in its non-native range within North America. In soils from North America, *C. maculosa* cultivated soil biota that had increasingly positive feedbacks on its growth, which may contribute to the success of this species on this continent (Callaway et al. 2004).

8.5 Policy and Legislation for Invasive Plants

North America has accumulated more invasive plant and animal species than any other continent (Fig. 8.5), and non-native species numbers are projected to continue to increase over the coming decades (Hulme 2009; Seebens et al. 2017, 2021). National legislation and international agreements have been developed in the last 100 years in attempts to reduce threats from non-native species to biodiversity, the economy, and human well-being (McGeoch et al. 2010; Seebens et al. 2017). Without legislation and international agreements, the number and impact of invasive species would probably be much greater (Seebens et al. 2017). Countries in North America are addressing non-native species in a variety of ways (Table 8.2), and there is a patchwork of additional legislation at state and local levels (Pyke et al. 2008; McGeoch et al. 2010). Much of this legislation focuses on prevention measures, as these are more cost-efficient and effective than combatting invasive species after their establishment and bearing the environmental and economic costs of invasion. Prevention measures are

Fig. 8.5 Predicted developments of alien, vascular plant species numbers on different continents until 2050. The dots represent means of up to 100 model runs. The shaded area represents the full range of predicted trajectories. Excerpted from Seebens et al. (2021)

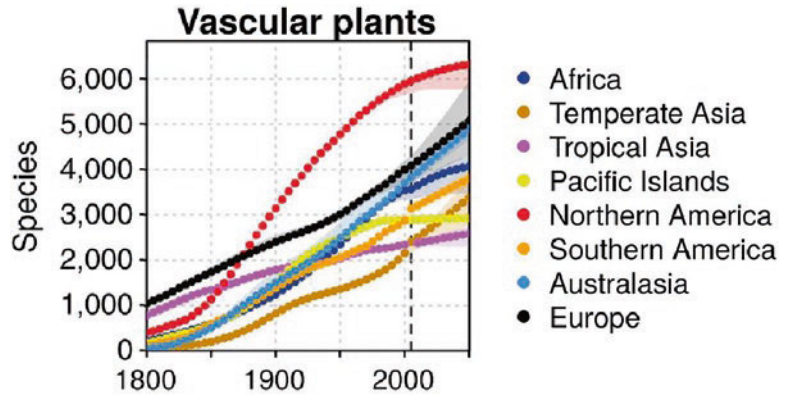


Table 8.2 Websites and examples of legislation for information on invasive plants by country

Country	Government website(s) for more information	Examples of national-level legislation
USA	https://www.fws.gov/invasives/laws.html	Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990
	https://plants.sc.egov.usda.gov/java/	Lacey Act
		Executive Order 13112
		Nutria Eradication Control Act
		Alien Species Prevention and Enforcement Act
Canada	https://www.canada.ca/en/services/environment/wildlife-plants-species/invasive-species.html	Plant Protection Act
		National Invasive Alien Species Strategy
Mexico	https://www.cbd.int/invasive/doc/legislation/Mexico.pdf	Bioinvasion and Global Environmental Governance: The Transnational Policy Network on Invasive Alien Species
		Agencies involved in Policy Network:
		1. The National Commission for Agricultural and Animal Health (CONASAG)
		2. The National Commission for the Knowledge and Use of Biodiversity (CONABIO)
		3. The Secretary of Environment and Natural resources (SERMANAT)
	4. The Federal Office for Environmental Protection (PROFEPA)	
	5. National Commission on Aquaculture and Fisheries (CONAPESCA)	

diverse, ranging from prohibitions on import, possession, or release of certain species to education to prevent accidental introduction of a species by the public (Pyke et al. 2008). Rapid response to initial sightings of a non-native plant species can be important for preventing subsequent invasion. For example, *Caulerpa taxifolia*, an invasive marine algae, was discovered in California in June 2000. Because *C. taxifolia* had a well-known 15-year history of spread in the Mediterranean Sea, this species was already on

the US Federal Noxious Weed List in 1999. This awareness facilitated mobilization of a large number of state, federal, and local agencies, as well as private groups and non-governmental organizations (Anderson 2005), and the two populations in California were considered eradicated in June 2006 (NOAA 2019).

In this era of globalization, it is projected that naturalization of non-native species will continue in North America. At the same time, as greenhouse gas emission rates continue to rise, climate

change is also increasingly affecting North America's ecosystems and the economy. Invasive plants and climate change are often treated as important, but independent, environmental issues. To date, there has been limited investment into forecasting how global climate change could shape future invasions, or how invasive species may affect the magnitude, rate, and impact of climate change (Pyke et al. 2008; Ricciardi et al. 2017). Thus, as new policies are developed in North America for invasive species, it will be beneficial to consider the implications of climate change and to develop policies that consider the interactions between invasive species and climate change that may combine to increase invasion risk to native ecosystems (Pyke et al. 2008; Bradley et al. 2009; Ricciardi et al. 2017). A changing climate creates risk as the climatic range for a given invasive species may expand into some new areas, but may also create opportunities for ecosystem restoration on invaded lands that have become climatically unsuitable for the invasive species (Bradley et al. 2009). Bradley et al. (2009) found that climate change can result in the potential for both range expansion and contraction of invasive plants in the western United States using habitat suitability modeling. Their analysis suggested *Centaurea solstitialis* and *Tamarix* spp. ranges are likely to expand with climate change, whereas *Bromus tectorum* and *Centaurea stoebe* are likely to shift in range, leading to both expansion and contraction (Bradley et al. 2009).

8.6 Conclusions

North America has more recorded naturalized plants than any other continent, and this number is expected to rise in the future as a result of human-related activities like transportation, agriculture, and climate change (van Kleunen et al. 2015; Pyšek et al. 2017; Ricciardi et al. 2017). The naturalization of these non-native species is often attributed to plant life history traits, and in North America, habitat legacy, propagule pressure, and residence time have been found to be important driving forces for non-native species to

become invasive (Pyšek et al. 2015). These species are often distributed disproportionately across the continent, with the majority of non-native species being found in the colder temperate and Mediterranean climate zones (Pyšek et al. 2017). Invasive non-native plants threaten ecosystems, habitats, and native species and are key drivers of human environmental change in North America. Challenges associated with plant invasions are likely to grow, as international trade continues and environmental changes influence the rate and consequences of future invasions (Pyke et al. 2008; Ricciardi et al. 2017).

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Plant Invasions in South America

9

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Abstract

Although South America is the fourth largest continent, it houses about 60% of the global terrestrial life and the highest number of plant species. Besides its great native biodiversity, there are an unknown number of introduced non-native plants and at least 2,677 known naturalized non-native plants in South America. Despite the growing knowledge on the richness and general status of non-native species, the real extent of distribution, abundance, and effects of invasive plants in South America are largely unknown. Here, we used country-level data on the number and identity of naturalized plant species to test which factors were related to non-native plant naturalization in the continent. To do so, we (i)

compiled a list of the most prominent invasive plants in the continent and (ii) reviewed the existing legislation in place to prevent and manage plant invasions. We found that mean latitude and number of bioclimates were good predictors of naturalized plant richness. We also found that plant invasions have pervasive impacts in South American ecosystems, but that the real magnitude of the impacts was vastly unknown because very few invasive species and invaded ecosystems have been studied. We also found that South American countries have legislations in place to manage plant invasions, but there were no integrated efforts across the countries to collaboratively address biological invasions. In conclusion, we show that there is information about the identity and distribution of most invasive

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plants, but there is a lack of comprehensive understanding of the impacts and future consequences on biodiversity and human well-being. We also highlight the importance of a more collaborative approach to prevent and manage invasions in the continent.

Keywords

Biological invasions · Invasive alien species · Invasive non-native species · Naturalized plant species · Established plant species

9.1 Introduction

South America is one of the most diverse continents on Earth with a wide range of geological formations, climates, and ecosystems. Even though it is the fourth largest continent, it houses about 60% of the global terrestrial life and the highest number of vascular plant species. South America is home to more than 82,000 plant species, 90% of which are endemic to the continent (Zappi et al. 2015; Ulloa et al. 2017). However, there are an unknown number of introduced non-native plants and at least 2677 known naturalized non-native plants in South America according to the Global Naturalized Alien Flora (GLONAF) (van Kleunen et al. 2019; Pyšek et al. 2019) and 1720 species according to the Global Register of Introduced and Invasive Species (GRIIS) (Pagad et al. 2018). If non-native plants were added to the regional floras, they would represent at least 1.4% of the total flora of the continent (Pyšek et al. 2019) and up to 7% of the flora of some South American ecosystems (e.g., Brazilian Pampas) (Zenni 2015).

Despite existing comprehensive lists of naturalized species for South America (van Kleunen et al. 2015; Pagad et al. 2018; Pyšek et al. 2019), there is currently a lack of a comprehensive list of invasive non-native plants at a continent level. There are continent-level lists of invasive plant species only for specific groups (e.g., Simberloff et al. 2010). Also, there are several country-level lists of naturalized and invasive non-native species. For instance, published reports indicate 573

naturalized plant species and 194 invasive plant species for Brazil (Zenni and Ziller 2011; Zenni 2015; Ziller et al. 2018). Fuentes et al. (2013) and Pauchard et al. (2019) listed 743 naturalized plant species for Chile, but the number of invasive species is currently unknown. A recent publication indicated the occurrence of 1,401 non-native plant species in Argentinean National Parks, but there was no classification in terms of naturalized or invasive species (Gantchoff et al. 2018). Moreover, these reports are not consistent in terms of breadth and depth of data collection or in terms of definitions adopted to classify species as invasive. For instance, the I3N-Horus Institute database of invasive species in Brazil (<http://i3n.institutohorus.org.br/www>) includes both species that are currently invasive in the country and species that are currently naturalized in Brazil but invasive elsewhere. The same was done for Chile (Fuentes et al. 2013), but not for Argentina (Gantchoff et al. 2018).

Despite the growing knowledge on the richness and general status of non-native species in South America, the real extent of distribution, abundance, and impacts of invasive plants in the continent is largely unknown. Here, we aimed to (1) synthesize the main patterns and correlates of naturalized plants in South America; (2) summarize the status of the most relevant invasive species in different ecosystems of South America; (3) synthesize the current knowledge on the impacts these species are having on native species, communities, and ecosystems; and (4) synthesize the existing legislation in place to manage invasive plants and invasion processes. Our approach was limited by data availability, as comprehensive data was lacking for several countries.

9.2 Data Sources

9.2.1 Main Patterns and Correlates of Naturalized Plants in South America

We used the GRIIS database for South American countries to list the naturalized non-native plant species on the continent. GRIIS was hosted at

<http://griis.org>, and the search was performed on April 23, 2019. Data were available for Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Guyana, Paraguay, Peru, Uruguay, and Venezuela. We included all records, instead of verified records only, because of the heterogeneity in number of experts validating data for each country. First, we collected geographic and demographic data for each country using official online sources (e.g., government websites). We collected area of the country (km²), population size, number of bioclimates as a proxy for environmental heterogeneity in the country, mean latitude, and 2017 Human Development Index (HDI) as a proxy for country economic wealth. Ecological, geographical, and historical factors have been shown to contribute to non-native biotas.

To test if the geographic and demographic data had an effect on the richness of each naturalized flora, we performed a linear model using naturalized species richness as the dependent variable and area of the country, number of bioclimates, mean latitude, and HDI as independent variables. We did not include population size and European colonizing country because of the high correlation of the former with country area and the extremely low variability of the latter. From the full model, we chose the best model by AIC (Akaike information criterion) using a stepwise algorithm. These analyses were performed in the software R version 3.5.2.

To evaluate patterns of the community of naturalized species in South American countries, we first performed a non-metric multidimensional scaling (NMDS) analysis using a matrix of presence and absence of naturalized species per country (community matrix). To analyze possible mechanisms explaining similarities among naturalized floras, we performed a permutational multivariate analysis of variance (Permanova) using the community matrix as dependent variable and area of the country, population size, number of bioclimates, mean latitude, HDI, and European colonizing country as independent variables. These analyses were performed in R version 3.5.2 using the package *vegan* version 2.5-4 (Oksanen et al. 2019).

9.2.2 Status and Current Knowledge of the Most Relevant Invasive Plants in the Native Ecosystems of South America

After the initial analysis of naturalized floras in each country, we used our expert knowledge to select the most relevant invasive non-native species in ecosystems of each country. We did not aim for a comprehensive list of invasive species, but for a representative list of the species with more information available and the highest perceived invasiveness and impact on native ecosystems. For each invasive species identified, we gathered and reviewed the published literature on the impacts of these species. We did this for Argentina, Brazil, Chile, Ecuador, and Venezuela because these were the countries for which we had expert in-depth knowledge. Attempting this method for countries we lack in-depth expertise would be a futile effort and probably result in incorrect assumptions and views.

9.2.3 Existing Legislation to Manage Invasive Plants and Invasion Processes

Finally, we reviewed the existing legislation of each country for managing plant invasions, including regulation of prevention, early detection, rapid response, control, use, and eradication efforts. We also did this only for Argentina, Brazil, Chile, Ecuador, and Venezuela.

9.3 Main Patterns and Correlates of Naturalized Plants in South America

GRIIS registered 553 naturalized plant species in Argentina, 247 in Bolivia, 503 in Brazil, 723 in Chile, 265 in Colombia, 348 in Ecuador, 166 in Guyana, 72 in Paraguay, 288 in Peru, 61 in Uruguay, and 219 in Venezuela (Figs. 9.1 and 9.2) for a total of 1720 naturalized non-native plant species (some species are naturalized

in multiple countries). The linear model with the lowest AIC (most parsimonious model) included mean latitude and number of bioclimates as predictors of naturalized plant richness ($F_{2,8} = 5.431$, $p = 0.03$). Country size and population size did not relate to naturalized species richness. The model explained 57.6% of the variation in the data ($r^2 = 0.5759$). Naturalized species richness was negatively related to mean latitude and positively related to number of biomes, and these effects were independent of country size or population size (Fig. 9.2).

Tropical South America (between zero and -23.5° latitude) has two or three times fewer naturalized non-native plants than temperate South America (latitude below -23.5°) despite its greater area. Previous research for Brazil at the biome level confirms a similar tendency of fewer naturalized species towards the Amazon and Pantanal regions (Zenni 2015). This difference probably results from long-term and more widespread anthropogenic-related pressures on natural ecosystems in the southern and southeastern regions of the continent. On one hand, Chile has lost 55% of the native forests to human-related activities, and 34% of the remaining native forests occur in fragmented landscapes (Neira et al. 2002), whereas in Argentina large areas of Chaco and Espinal have been converted into agriculture and cattle pastures and some estimates indicate less than 40% of the native forest still exists (Guida-Johnson and Zuleta 2013 and references within). On the other hand, the Amazon region (including large parts of Brazil, Colombia, Ecuador, Peru, and Venezuela) is estimated to have 80% of its tropical forest remaining (WWF 2019). Pantanal is the least converted biome in Brazil with 85% of the ecosystem remaining (CSR/IBAMA 2011). Considering current and historical anthropogenic effects on natural ecosystems across South America and the existing synergies between non-native species and habitat degradation (Richardson and Pyšek 2012), it is expected that more naturalized species are found on more ecosystems with higher human pressure. However, we are also aware that GRIIS is currently incomplete for several South American countries, including Ecuador and

Venezuela. For instance, GRIIS does not register *Trifolium repens* and *Roystonea oleracea* for Ecuador, two known naturalized species. Also, there are several studies dedicated to non-native species in the southern regions of the continent (e.g., de Andrade Frehse et al. 2016).

Among naturalized plants in South America, 41.2% were reported for more than one country ($n=709$), but only one species, *Sorghum halepense*, was reported for all countries from which we had data. Thirty-three plant species were reported for seven or more countries (Table 9.1). The most widespread grouping of non-native plants in the continent according to this analysis was grasses, followed by trees. Most of the species ($\sim 59\%$), however, were reported for a single country, possibly suggesting that most plant introductions in South America were independent introductions from other continents rather than movement (intentional or accidental) within South America by human-related routes or pathways. The country-level variation of the naturalized flora of South America varies by latitude and number of bioclimates in a country (Fig. 9.3), showing that climate and environmental heterogeneity have an important role on the identity of species that are introduced and naturalized in different regions.

The Convention on Biological Diversity defined invasive species as “species whose introduction and/or spread outside their natural past or present distribution threatens biological diversity.” GRIIS lists 783 naturalized plants in South America (45.5% of the total 1720) as having evidence of impacts published in the peer-reviewed literature or technical reports. Therefore, from this perspective, these species could be classified as invasive. However, the current population status for most of the species is poorly known, and most of the evidence gathered so far for impact are qualitative and indirectly observed (Zenni et al. 2016). For example, for Argentina 47.6% of the naturalized species were reported in GRIIS as having a negative impact, but for Paraguay (a neighboring country) none of the species were reported as having evidence of any negative impact. Both countries share many invasive species. In the tropical region of the continent, 1.8%

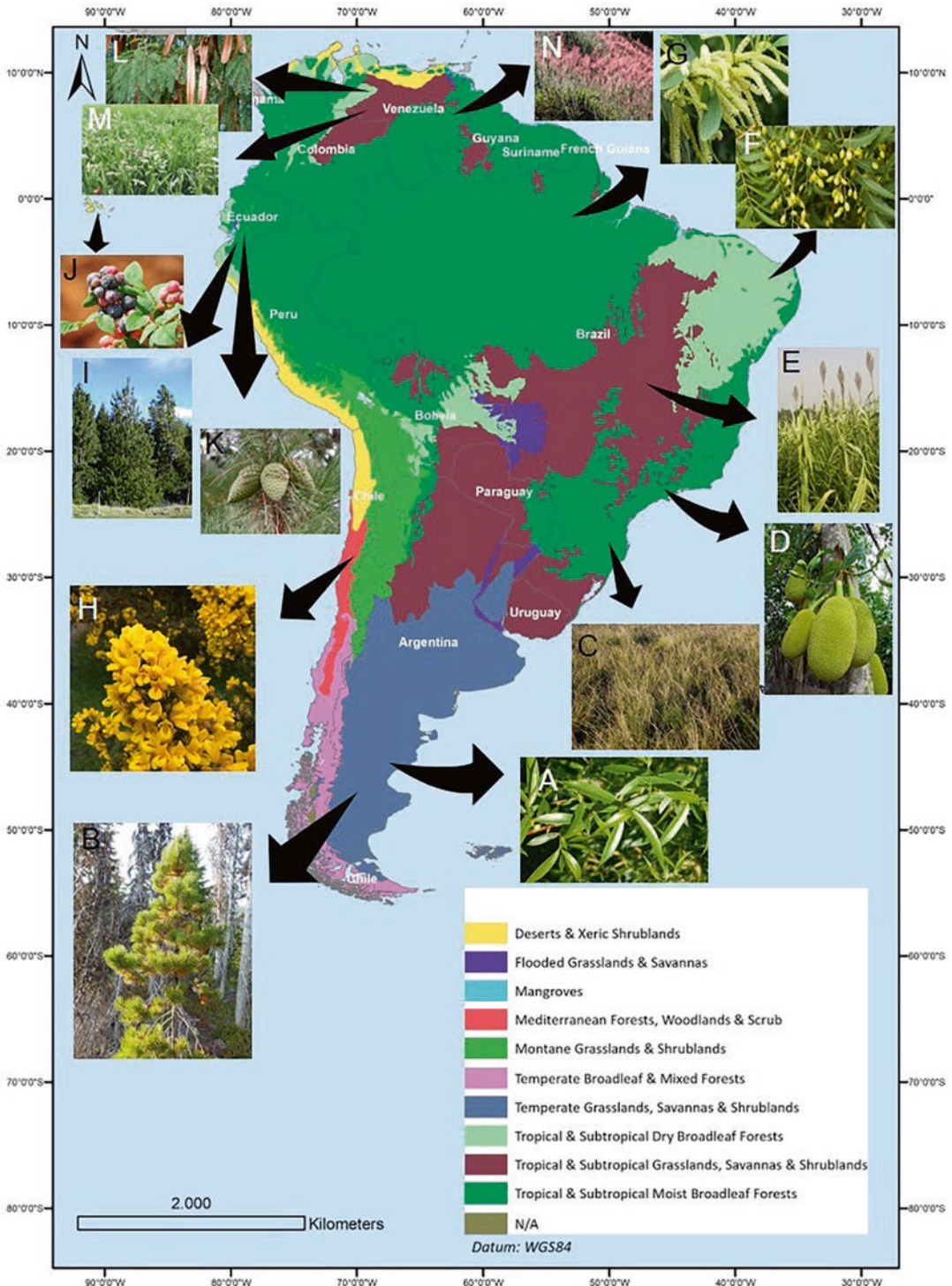


Fig. 9.1 Infographic of invasive non-native plants in South American biomes. Each letter on the picture corresponds to an invasive non-native plant in a South American country. A, *Salix fragilis* – *Salix alba* hybrid complex; B, *Pinus contorta*; C, *Eragrostis plana*; D, *Artocarpus heterophyllus*; E, *Arundo donax*; F, *Azadirachta indica*; G, *Acacia mangium*; H, *Ulex europaeus*; I, *Pinus patula*; J,

Rubus niveus; K, *Pinus radiata*; L, *Leucaena leucocephala*; M, *Melinis minutiflora*. (Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, © OpenStreetMap contributors, and the GIS User Community)

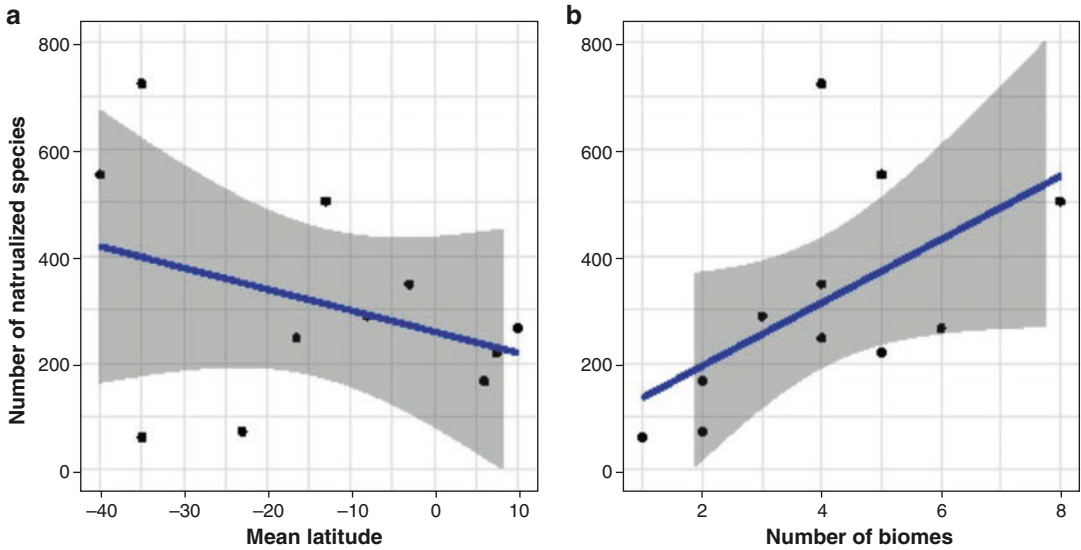


Fig. 9.2 Variation in naturalized species richness in South American countries as a function of (a) mean latitude of the country and (b) number of biomes (environ-

mental heterogeneity). Dots are South American countries; lines represent the linear model adjustments, and gray areas are 95% confidence intervals

of the naturalized species were said to have evidence of negative impacts, whereas for Peru none of the naturalized species were reported as displaying any evidence of negative impact. Consequently, we are still unable to quantify at the continent level, with an acceptable degree of confidence, the actual number of invasive species (the subset of naturalized species that are threatening ecosystems, habitats or species) and their impacts on natural ecosystems.

9.4 Status and Current Knowledge of the Most Relevant Invasive Plants in the Native Ecosystems of South America

We identified 46 species as the most relevant invasive plants in the South American ecosystems (Table 9.2). Most of the non-native species were identified as prominent invaders only for one country. Five species were considered prominent invaders in more than one country (*Melinis minutiflora*, *Azadirachta indica*, *Leucaena leucocephala*, *Ulex europaeus*, and *Pinus contorta*) suggesting that, although there are many shared

naturalized plants among South American countries, the invasive species are more regionalized. Seven of these species (16%) are also among the most widespread naturalized species in the continent including *Calotropis procera*, *Hyparrhenia rufa*, *Leucaena leucocephala*, *Pennisetum clandestinum*, *Poa annua*, *Ricinus communis*, and *Ulex europaeus* (Table 9.1). Interestingly, while most of the widespread naturalized plants were grasses (46%), the majority of the most relevant invasive species were trees (41%). Only 21% of the most widespread plants were trees. It is unclear if trees indeed have larger impacts than grasses and shrubs, or if trees are more easily perceived as invasive species.

9.4.1 Southern Argentina

Impacts have not been the main focus of research on invasive species in western Patagonia, but there are some key studies on the topic centered on woody species. Some of the clearest examples, due to extension of their invasions, are *Salix* and Pinaceae. The *Salix fragilis*-*Salix alba* hybrid complex invades large number of streams and rivers, and currently it is rare to see a river with-

Table 9.1 Non-native plant species with the most records of naturalization in South American countries

Species	Family	Life form	Number of countries
<i>Sorghum halepense</i>	Poaceae	Grass	10
<i>Arundo donax</i>	Poaceae	Grass	9
<i>Cynodon dactylon</i>	Poaceae	Grass	9
<i>Ricinus communis</i>	Euphorbiaceae	Shrub	9
<i>Cenchrus ciliaris</i>	Poaceae	Grass	8
<i>Cyperus esculentus</i>	Cyperaceae	Grass	8
<i>Echinochloa colona</i>	Poaceae	Grass	8
<i>Eichhornia crassipes</i>	Pontederiaceae	Herb	8
<i>Eleusine indica</i>	Poaceae	Grass	8
<i>Gliricidia sepium</i>	Fabaceae	Tree	8
<i>Leucaena leucocephala</i>	Fabaceae	Tree	8
<i>Melia azedarach</i>	Meliaceae	Tree	8
<i>Melinis repens</i>	Poaceae	Grass	8
<i>Pennisetum clandestinum</i>	Poaceae	Grass	8
<i>Plantago major</i>	Plantaginaceae	Herb	8
<i>Poa annua</i>	Poaceae	Grass	8
<i>Bidens pilosa</i>	Asteraceae	Herb	7
<i>Brachiaria mutica</i>	Poaceae	Grass	7
<i>Calotropis procera</i>	Apocynaceae	Tree	7
<i>Cenchrus echinatus</i>	Poaceae	Grass	7
<i>Cyperus rotundus</i>	Cyperaceae	Grass	7
<i>Datura stramonium</i>	Solanaceae	Shrub	7
<i>Delonix regia</i>	Fabaceae	Tree	7
<i>Eucalyptus camaldulensis</i>	Myrtaceae	Tree	7
<i>Grevillea robusta</i>	Proteaceae	Tree	7
<i>Hyparrhenia rufa</i>	Poaceae	Grass	7
<i>Kalanchoe pinnata</i>	Crassulaceae	Herb	7
<i>Momordica charantia</i>	Cucurbitaceae	Herb	7
<i>Oeceoclades maculata</i>	Orchidaceae	Orchid	7
<i>Pennisetum polystachion</i>	Poaceae	Grass	7
<i>Pistia stratiotes</i>	Araceae	Palm	7
<i>Portulaca oleracea</i>	Portulacaceae	Shrub	7
<i>Ulex europaeus</i>	Fabaceae	Shrub	7

Data from GRIIS for Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, Guyana, Paraguay, Peru, Uruguay, and Venezuela

out *Salix* in the steppe biome (the largest biome in Patagonia). This invasion modifies hydrology and threatens the native *Salix humboldtiana*, as only a few populations still remain in the region. The non-native species *Salix* is threatening *S. humboldtiana* both by occupying the area where the native *Salix* grows and by hybridizing, which can have irreversible impacts (Datri et al. 2017).

Pinaceae has been introduced in the region for forestry purposes, and some of them are currently highly invasive in both open areas (steppe) and in forests. Pinaceae invasion in native forest (like

Pseudotsuga menziesii in Nothofagus forests) presents a unique challenge since pines can replace the native vegetation in the forest, and they can also change the structure of the native vegetation in the areas they colonize (Paritsis et al. 2018). In the steppe, other pine species invade, mainly *Pinus contorta*, and these have been shown to reduce native biodiversity and increase risks of fires, cause threats to human well-beings and forestry plantations, and, in turn, promote further pine invasions (Taylor et al. 2016; Taylor et al. 2017).

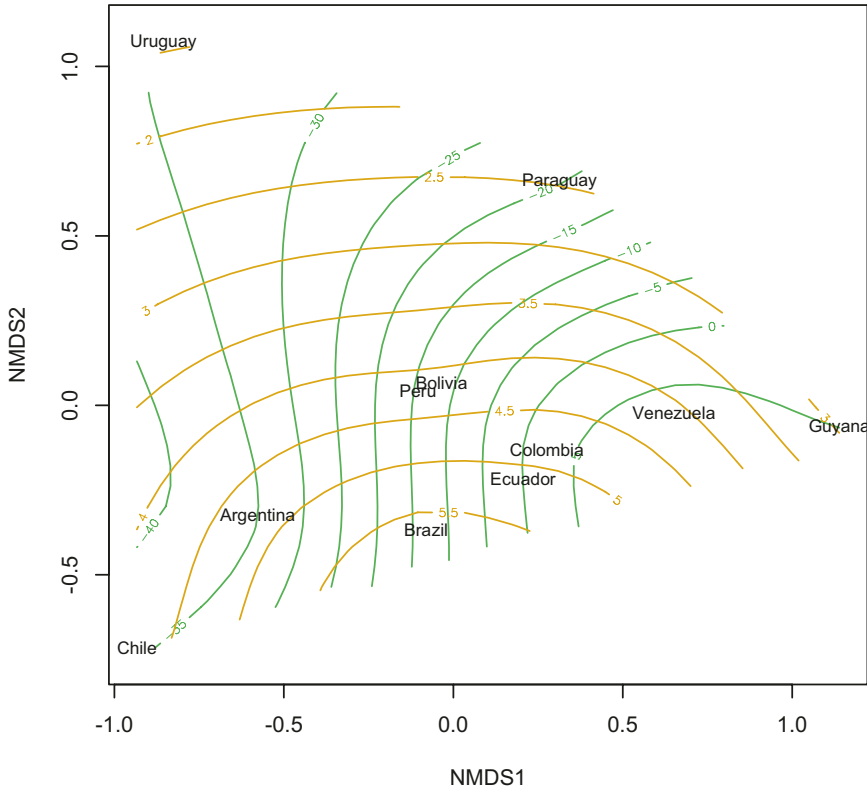


Fig. 9.3 NMDS (non-metric multidimensional scaling) of the naturalized flora of South American countries ($k = 3$, stress = 0.03). Green lines are latitude isoclines, and brown lines are number of bioclimate isoclines. Latitude

explains most of the variation in the first axis (NMDS1), whereas number of bioclimate (environmental heterogeneity) explains most of the variation in the second axis (NMDS2)

9.4.2 Brazil

Invasive trees can have pervasive negative impacts on different tropical and subtropical ecosystems in Brazil (de Abreu and Rodrigues 2010; de Sa Dechoum et al. 2015b; Lazzarin et al. 2015; Bergallo et al. 2016). Those impacts are better documented for the Atlantic Rainforest and for the Seasonal Deciduous Forest in South and Southeastern Brazil. Although it is common to associate the impacts of invasive trees to treeless ecosystems such as grassland and coastal scrub, most papers about the impacts of invasive trees in Brazil have reported negative impacts on the structure and dynamics of forest ecosystems. Invasive non-native trees can change abiotic conditions and regeneration patterns of invaded ecosystems. They may also change species abundance, richness, and composition and the

structure of different vegetation types in Brazil (e.g., de Sa Dechoum et al. 2015a; de Sa Dechoum et al. 2015b; de Abreu and Durigan 2011).

The environmental impacts more often associated with biological invasions by herbs and grasses refer to dominance and displacement of indigenous species, as well as direct impacts on ecosystems (Pivello et al. 1999; Gorgone-Barbosa et al. 2015; Zenni et al. 2019). Allelopathy by invasive herbs prevents germination by other species, facilitating dominance (Gorgone-Barbosa et al. 2008; Mello and Oliveira 2016), while some species, especially grasses, alter natural fire regimes (Rossi et al. 2014; Gorgone-Barbosa et al. 2015) in fire-prone savannas and grasslands. Tall grasses such as *Arundo donax* generate structural habitat changes that affect and displace native animals (Simões et al. 2013). The impacts of

Table 9.2 Most prominent non-native plant invaders in South American ecosystems and the list of studies on ecology and impacts of these species

Country	Species	Region where invasive in the country	Biomes	References on impacts
Argentina	<i>Acacia longifolia</i>	East-central		Stellatelli et al. (2013)
Argentina	<i>Pinus contorta</i>	West-central	Temperate grasslands/steppe; alpine habitats, temperate forests	Urrutia et al. (2013), Taylor et al. (2016), and Franzese et al. (2017)
Argentina	<i>Salix fragilis</i> – <i>Salix alba hybrid complex</i>	West-central	Temperate grasslands/steppe; alpine, temperate forests	Datri et al. (2017)
Brazil	<i>Acacia mangium</i>	North; Southeast	Savanna; Atlantic rainforest	Aguiar et al. (2013) and Heringer et al. (2019)
Brazil	<i>Artocarpus heterophyllus</i>	Southeast; Northeast; South	Atlantic rainforest	Boni et al. (2009), de Abreu and Rodrigues (2010), Oliveira et al. (2011), Fabricante et al. (2012), Mileri et al. (2012), Fabricante (2014), Bergallo et al. (2016), Freitas et al. (2017), and de Oliveira (2018)
Brazil	<i>Arundo donax</i>	Central	Cerrado	
Brazil	<i>Azadirachta indica</i>	Northeast	Caatinga	
Brazil	<i>Casuarina equisetifolia</i>	South	Atlantic rainforest – coastal areas	
Brazil	<i>Elaeis guineensis</i>	Northeast	Atlantic rainforest	
Brazil	<i>Eragrostis plana</i>	South; Southeast	Pampa	Barbosa et al. (2012)
Brazil	<i>Furcraea foetida</i>	Northeast; Southeast; South	Atlantic rainforest – coastal areas	Barbosa et al. (2017a, 2017b)
Brazil	<i>Hedychium coronarium</i>	South; Southeast	Atlantic rainforest; Cerrado	de Castro et al. (2016)
Brazil	<i>Hovenia dulcis</i>	South	Atlantic rainforest	Dechoum et al. (2015a) and Lazzarin et al. (2015)
Brazil	<i>Leucaena leucocephala</i>	Southeast	Atlantic rainforest	Marques et al. (2014) and Mello and Oliveira (2016)
Brazil	<i>Ligustrum lucidum</i>	South	Atlantic rainforest	Hummel et al. (2014)
Brazil	<i>Megathyrsus maximus</i>	South	Atlantic rainforest; Cerrado	Mantoani et al. (2012)
Brazil	<i>Melia azedarach</i>	South	Atlantic rainforest	
Brazil	<i>Melinis minutiflora</i>	South, Central	Atlantic rainforest; Cerrado	Klink (1994), Hoffmann and Haridasan (2008), Martins et al. (2011), Lannes et al. (2012), de Mello et al. (2014), Rossi et al. (2014), Damasceno et al. (2018) and Zenni et al. (2019)
Brazil	<i>Pinus elliottii</i>	South; Southeast	Cerrado; Atlantic rainforest; pampa	de Abreu and Durigan (2011), Zenni and Simberloff (2013), and Bechara et al. (2013)
Brazil	<i>Pinus taeda</i>	South; Southeast	Atlantic rainforest; Pampa	Falleiros et al. (2011) and Zenni and Simberloff (2013)
Brazil	<i>Prosopis juliflora</i>	Northeast	Caatinga	
Brazil	<i>Prosopis pallida</i>	Northeast	Caatinga	
Brazil	<i>Tecoma stans</i>	South	Atlantic rainforest	
Brazil	<i>Terminalia catappa</i>	Southeast; South	Atlantic rainforest	

(continued)

Table 9.2 (continued)

Country	Species	Region where invasive in the country	Biomes	References on impacts
Brazil	<i>Tradescantia zebrina</i>	Southeast; South	Atlantic rainforest	
Brazil	<i>Ulex europaeus</i>	South	Pampa; Southern grasslands in Atlantic rainforest	
Brazil	<i>Urochloa decumbens</i>	South; Southeast; Central; North	Cerrado; Atlantic rainforest; Amazon Forest	Gorgone-Barbosa et al. (2008) and Lannes et al. (2012)
Brazil	<i>Urochloa brizantha</i>	Southeast; Central; Northeast; North	Cerrado; Atlantic Rainforest; Amazon Forest	Gorgone-Barbosa et al. (2015) and Damasceno et al. (2018)
Chile	<i>Pinus contorta</i>	South-central	Temperate grasslands/steppe; alpine habitats, temperate forests	Urrutia et al. (2013), Taylor et al. (2016), and Franzese et al. (2017)
Chile	<i>Acacia dealbata</i>	South-central	Temperate and Mediterranean forests	Fuentes-Ramírez et al. (2010), Fuentes-Ramírez et al. (2011) and Aguilera et al. (2015)
Chile	<i>Teline monspessulana</i>	South-central	Temperate and Mediterranean forests	García et al. (2007), Pauchard et al. (2008), and García et al. (2015)
Chile	<i>Ulex europaeus</i>	South-central	Temperate and Mediterranean forests	Altamirano et al. (2016)
Ecuador	<i>Roystonea oleracea</i>	Southwestern	Flooded grasslands and savannas	Herrera et al. (2017)
Ecuador	<i>Pinus patula</i>	Southern	Tropical and subtropical moist broadleaf forests	Aguirre et al. (2006), Chacón et al. (2009a), Narváez Riofrío (2015), Quichimbo et al. (2017), and Castillo et al. (2018), and Quiroz Dahik et al. (2018)
Ecuador	<i>Cinchona pubescens</i>	Galapagos	Deserts and xeric Shrublands	Jäger et al. (2007) and Jäger et al. (2013)
Ecuador	<i>Rubus niveus</i>	Galapagos	Deserts and xeric shrublands	Rentería et al. (2012)
Ecuador	<i>Setaria sphacelata</i>	South	Tropical and subtropical moist broadleaf forests	Günter et al. (2009), Palomeque et al. (2017), and Castillo et al. (2018)
Ecuador	<i>Eucalyptus saligna</i>	South	Tropical and subtropical moist broadleaf forests	Narváez Riofrío (2015) and Castillo et al. (2018)
Ecuador	<i>Pinus radiata</i>	South	Montane grasslands and shrublands	Middendorp et al. (2016)
Ecuador	<i>Melinis minutiflora</i>	South	Tropical and subtropical moist broadleaf forests	Palomeque et al. (2017)
Venezuela	<i>Kalanchoe x houghtonii</i> (<i>Kalanchoe daigremontiana</i>)	Northwestern; Margarita Island	Tropical and subtropical dry broadleaf; deserts and xeric shrublands	Chacón et al. (2009b), Herrera and Nassar (2009), Herrera et al. (2012), Herrera et al. (2016), and Herrera et al. (2018)
Venezuela	<i>Hyparrhenia rufa</i>	Central	Tropical and subtropical grasslands, savannas, and shrublands	San Jose and Farinas (1991), Baruch (1996), Bilbao et al. (1996), and Pieters and Baruch (1997)

(continued)

Table 9.2 (continued)

Country	Species	Region where invasive in the country	Biomes	References on impacts
Venezuela	<i>Pinus caribaea</i>	North central	Tropical and subtropical moist broadleaf forests Tropical and subtropical grasslands, savannas, and shrublands	Fassbender et al. (1979), Suarez et al. (2000), Gómez et al. (2008), Hernández-Hernández et al. (2008), Hernández Gil et al. (2009), Bueno and Baruch (2011), Aguilera et al. (2015), Baruch et al. (2016), Baruch et al. (2019)
Venezuela	<i>Melinis minutiflora</i>	Northwestern	Tropical and subtropical moist broadleaf forests	Bilbao and Medina (1990), Baruch (1996), Barger et al. (2003), and Ataroff and Naranjo (2009)
Venezuela	<i>Pennisetum clandestinum</i>	Northwestern	Tropical and subtropical moist broadleaf forests	Ataroff and Naranjo (2009)
Venezuela	<i>Azadirachta indica</i>	Northwestern	Tropical and subtropical dry broadleaf forests	Vera et al. (2007) and Villarreal et al. (2010)
Venezuela	<i>Leucaena leucocephala</i>	Northwestern	Tropical and subtropical dry broadleaf forests	Razz and Clavero (2006)
Venezuela	<i>Calotropis procera</i>	Northwestern; Margarita Island	Tropical and subtropical dry broadleaf forests; deserts and xeric shrublands	Johnston (1908) and Tezara et al. (2011)
Venezuela	<i>Ricinus communis</i>	Northwestern	Tropical and subtropical dry broadleaf forests; deserts and xeric shrublands	Alfonso (2003) and Villarreal et al. (2010)
Venezuela	<i>Poa annua</i>	Southeast	Tropical and subtropical grasslands, savannas, and shrublands	Chitty and Nozawa (2010)
Venezuela	<i>Polypogon elongatus</i>	Southeast	Tropical and subtropical grasslands, savannas, and shrublands	Chitty and Nozawa (2010)
Venezuela	<i>Rumex acetosella</i>	Northwestern	Montane grasslands and shrublands	Llambí et al. (2018)

greater concern directly affect ecosystem functioning, including significant changes in the nutrient pool and flux, changes in habitat, and disturbance regimes (Barbosa et al. 2010; Rossi et al. 2014; Gorgone-Barbosa et al. 2015; de Castro et al. 2016; Damasceno et al. 2018; Zenni et al. 2019). Invasion by grasses and herbs generates economic impacts due to the costs of intensive control in agricultural areas as well as, for example, along roads, especially privatized toll roads, and environmental restoration projects.

Currently in Brazil, two of the most prominent invasive non-native conifers are *Pinus taeda* and

Pinus elliottii (Simberloff et al. 2010; Zenni and Ziller 2011). The aspects related to the success of biological invasions of these two *Pinus* species are seed dispersal by wind, intensive cultivation, and the capacity to tolerate high levels of anthropogenic disturbance (Falleiros et al. 2011; Valduga et al. 2016). One of the impacts established for *P. elliottii* is the change in growth dynamics of native plants by altering its vegetation coverage (Falleiros et al. 2011). Additionally, it is also known that *P. taeda* and *P. elliottii* can cause changes in composition and functional traits of native vegetation (de Abreu and Durigan 2011).

9.4.3 Ecuador

The state of knowledge of plant invasions in Ecuador contrasts significantly between the continent and the insular region, represented by the Galapagos Islands. Most of the scientific articles on biological invasions in Ecuador are on the Galapagos; very few studies have assessed invasion status of exotic species in mainland Ecuador. There is no complete official list of exotic plant species for Ecuador yet. A preliminary version of this list suggests that there are 677 introduced plant species in mainland Ecuador. Of these, 13% (88 species) have been reported as invasive in other regions of the world, e.g., *Arundo donax*, *Ulex europaeus*, and *Leucaena leucocephala*. Species of temperate origin such as *Cerastium glomeratum*, *Poa annua*, *Holcus lanatus*, *Trifolium repens*, *Plantago lanceolata*, and *Rumex acetosella* have a wide distribution and occur very frequently in mainland Ecuador (Sandoya et al. 2017). However, the impacts of these invasive species on the structure and functions of ecosystem are still unknown.

In Montane Forests (also mainland Ecuador), non-native tree species of the genera *Pinus* and *Eucalyptus* are the most frequent species used in reforestation programs. Previous studies have suggested that these forestry plantations (e.g., *Pinus patula*) could affect the fertility of the soil, by reducing the cation exchange capacity (Chacón et al. 2009a), and have negative effects on the hydrological balance and biodiversity. In Dry Broadleaf Forests, located in the coastal region, *L. leucocephala* and *Urochloa maxima* can be observed naturalized along highways and roads; but there are no studies that formally assess the status of these species. At Santay Island, a Ramsar wetland and a national protected area in this region (Flooded Grasslands and Savannas), the invasion by an ornamental palm species (*Roystonea oleracea*) native from Caribbean was reported (Herrera et al. 2017), but the impact of this invasion is unknown.

In the Ecuadorian Amazon, the state of plant invasions is almost completely unknown. There have been reports in Napo province (Tropical

Lowland Humid Forest) that, along streams, naturalized populations of *Hedychium coronarium* and *Pennisetum purpureum* can be observed, but there are no publications on this. In the Biosphere reserve of Podocarpus (Tropical Montane Humid Forest) in Zamora Chinchipe province (southern Ecuador), eight non-native species of trees and herbs have been reported to have been introduced for agricultural purposes, but the abundance and the potential impacts of these introductions are unknown (Schüttler and Karez 2008).

Contrary to mainland Ecuador, the Galapagos Islands have a detailed and permanently updated inventory of non-native plant species and their current status. In the Islands, 881 non-native plant species have been recorded (Jaramillo Díaz et al. 2018). Guézou et al. (2010) reported at least 264 naturalized plant species in Galapagos. Biological invasions are considered the most serious threat to the biodiversity of Galapagos, where the non-native taxa now outnumber the native ones.

9.4.4 Venezuela

The first and only official list of exotic species in Venezuela was published in 2001 by the Ministry of Environment (Ojasti et al. 2001). The report listed 985 non-native plant species, of which 165 (~17%) were considered naturalized. From these, 49 plant species had been reported to have invasive status in Venezuela (5% of all non-native species and 30% of the naturalized species). The data is well aligned with the GRIIS data shown above. A revision of the list provided by Ojasti et al. (2001) shows that the region with the highest number of invasive plants is the Venezuelan Llanos (15 species), followed by Venezuelan Andes (14 species). The revision also suggested that there are at least 1,305 non-native plant species in Venezuela (Herrera, I. et al. unpublished data), but there are currently only 20 scientific publications regarding the presence of non-native plant species in the country.

The invasive species reported as having definite impacts on Venezuelan ecosystems were *Eucalyptus robusta*, *Hyparrhenia rufa*,

Kalanchoe x houghtonii, *Melinis minutiflora*, *Pinus caribaea*, *Stapelia gigantea*, and *Rumex acetosella*. In the Biome Deserts and Xeric Shrublands, the hybrid *Kalanchoe x houghtonii* forms dense patches with several populations in the western part of the country and Margarita Island. This species can inhibit the recruitment rates of native plants (Herrera et al. 2016) and can also modify the nitrogen and carbon cycles in the soil (Herrera et al. 2018). Despite the negative impacts caused by *Kalanchoe x houghtonii* in the continent, the consequences of this invasion in Margarita Island are still unknown.

In the Dry Broadleaf Forests, including Margarita Island Dry Forests, the invasive species with the widest distribution is *Leucaena leucocephala*. Despite its record as a noxious invasive plant in several parts of the world, studies in Venezuela are focused on improving its production and propagation as an alternative forage for cattle (e.g., Sánchez-Paz and Ramírez-Villalobos 2006; Medina et al. 2007). In the Savannas and deforested Moist Broadleaf Forests in mid-elevation areas over 600 m a.s.l., located in the Coast and Andean Cordillera, the African grass *M. minutiflora* generates mono-specific patches after any disturbance (e.g., fire, overgrazing), which limits the regeneration of native vegetation (Barger et al. 2003). In Los Llanos, lowland savannas, another African grass, *H. rufa*, is the dominant invasive species and replaces the native grass *Trachypogon* spp. Baruch (1996) suggested that anthropogenic fire regime was the main facilitator for the establishment of this species. Once established, *H. rufa* replaces native savannas by modifying the microclimate, decreasing the availability of nutrients, and increasing the intensity and frequency of fire cycles. In Alpine ecosystems of the Venezuelan Andes, *Rumex acetosella* invades a broad altitudinal range from 2800 to 4300 m (I. Herrera, unpublished data). In this ecosystem, *R. acetosella* can be a dominant species, reaching up to 45% of the total plant density (Llambí et al. 2018). High densities of *R. acetosella* can have a negative effect on abundance and richness of native plant species (Llambí et al. 2018).

9.5 Existing Legislation to Manage Invasive Plants and Invasion Processes

All countries mentioned in this review have legislations in place to manage biological invasions (Table 9.3). The legislation ranges from international conventions (e.g., Convention on Biological Diversity), National Constitutions (e.g., right of the people to a sustainable and clean environment), laws (e.g., prohibition of non-native species in strictly protected areas), and action plans (e.g., Brazilian national plan for *Sus scrofa*). Several countries (e.g., Brazil, Argentina) also have official national strategies for invasive non-native species (Table 9.3).

Some countries and territories also have official lists of invasive species. The southern states of Brazil (Rio Grande do Sul, Santa Catarina, and Paraná) have official lists of invasive species. Venezuela also has an official list (Ojasti et al. 2001). For Ecuador, only the Galapagos Islands has such a list, and a complete analysis of the biological invasions in the archipelago was recently published (de Lourdes Torres and Mena 2018). Additionally, the Galapagos Islands has a special administrative regime with institutions in charge of the prevention, monitoring, and control of non-native species as the Galapagos Agency for Biosecurity (ABG) and research institutions such as the Charles Darwin Foundation (CDF) or the Galapagos National Park.

In continental Ecuador, the Ministry of Environment with the support of other state institutions is responsible for the regulation and management of non-native species in the country, and they have developed several legal instruments in recent years. However, the risk assessments have not been put in practice, illustrating the lack of articulation between the laws and the practical application of the monitoring and management of introduced species. As mentioned before, this has led to a lack of completeness of information and uncertainty of the role of invasive plant species in Ecuador.

The legal framework for invasive non-native species in Venezuela is based on article 127 of the Constitution, which states that it is a right and

Table 9.3 Existing legislation related to plant invasions in South America

Country	Type	Government body	Number	Year of publication	Short description
Argentina	Constitution	Federal		1994	National Constitution
Argentina	Law	Federal	22415	1981	Customs law
Argentina	Law	Federal	22351	1981	National Parks legislation
Argentina	Law	Federal	24375	1994	Convention on Biological Diversity
Argentina	Law	Federal	27346	2015	Nagoya Protocol
Argentina	Law	Federal	26331	2007	Creates the "Unidad de Coordinación del Programa MAB" (UCPMAB), El hombre y la Biósfera Program
Argentina	Law	Federal	26815	2012	Federal system of fire management
Argentina	Law	Federal	25675	2002	Environmental Protection Law
Argentina	Resolution	Federal	460/1999 SAyDS	1999	Aprueba el "Programa Nacional de Gestión de la Flora"
Argentina	Resolution	Federal	1766/2007 SAyDS	2007	Regulates importation and exportation of wildlife
Argentina	Decree	Federal	234/12 COFEMA	2012	Management and control of <i>Didymosphenia geminata</i> and <i>Undaria pinnatifida</i>
Brazil	Decree	Federal	148	2010	Approves the text of the International Convention for the Control and Management of Ships' Ballast Water and Sediments
Brazil	Decree	Federal	6514	2008	Establishes sanctions and punitive measures for environmental issues
Brazil	Decree	Federal	4340	2002	Regulates the National Protected Area System
Brazil	Decree	Federal	2	1994	Approves the text of the International Convention on Biodiversity
Brazil	Normative Instruction	Federal	23	2014	Provides guidelines for the destination of wild animals that are apprehended, rescued by authorities, or handed in by the general public, including non-native species
Brazil	Normative Instruction	Federal	3	2013	Acknowledges wild boar as a harmful invasive species and provides guidelines for control
Brazil	Normative Instruction	Federal	141	2006	Regulates the management of synanthropic harmful animals, including invasive non-native species
Brazil	Normative Instruction	Federal	73	2005	Prohibits sales or breeding of giant African snails <i>Achatina fulica</i> in Brazil
Brazil	Law	Federal	9985	2000	Establishes the National Protected Area System, including a prohibition for the introduction of non-native species in protected areas
Brazil	Law	Federal	9605	1998	Defines actions as crimes against the environment, including the introduction of species without permits from the Federal Environmental Agency and the spread of non-native species
Brazil	Ordinance	Federal	58	2019	Approves the Action Plan for the control of cats (<i>Felis catus</i>) in the Fernando de Noronha – Rocas – São Pedro and São Paulo Environmental Protection Area and in the Fernando de Noronha National Park

(continued)

Table 9.3 (continued)

Country	Type	Government body	Number	Year of publication	Short description
Brazil	Ordinance	Federal	3639	2018	Approves the National Plan for the prevention, control, and monitoring of golden mussels (<i>Limnoperna fortunei</i>) in Brazil
Brazil	Ordinance	Federal	3642	2018	Approves the National Plan for the prevention, control, and monitoring of sun corals (<i>Tubastraea coccinea</i> and <i>T. tagusensis</i>) in Brazil
Brazil	Ordinance	Federal	3	2018	Approves the National Strategy on invasive non-native species
Brazil	Ordinance	Federal	4	2018	Institutes the Technical Advisory Group to oversee the implementation of the National Strategy on invasive non-native species
Brazil	Ordinance	Federal	232	2017	Approves the National Plan for the prevention, control, and monitoring of wild boars (<i>Sus scrofa</i>) in Brazil
Brazil	Ordinance	Federal	145	1998	Defines rules for the introduction, reintroduction, and transfer of fishes, crustaceans, mollusks, and aquatic macrophytes for aquaculture, excluding ornamental animals
Brazil	Ordinance	Federal	142	1994	Prohibits the introduction, transfer, cultivation, and sale of African catfish (<i>Clarias gariepinus</i>) and channel catfish (<i>Ictalurus punctatus</i>) in the Amazon and Paraguay river basins
Brazil	Resolution	Federal	7	2018	Instates the National Strategy on invasive non-native species (2nd edition), cancelling the former version
Brazil	Resolution	Federal	429	2011	Provides guidelines for the restoration of permanent preservation areas, acknowledging the benefits of invasive non-native species control
Brazil	Ordinance	State	14	2018	Establishes a State Program for the control of invasive non-native species
Brazil	Ordinance	State	59	2015	Publishes the official list of invasive non-native species for Parana state
Brazil	Ordinance	State	84	2015	Establishes a Technical Committee to review and formalize the State Program for invasive non-native species and deliver legal regulations
Brazil	Ordinance	State	79	2013	Publishes the official list of invasive non-native species for Rio Grande do Sul state
Brazil	Ordinance	State	19	2009	Establishes a State Committee for invasive non-native species
Brazil	Ordinance	State	192	2005	Regulates the control of invasive non-native species in protected areas managed by the state authority
Brazil	Resolution	State	8	2012	Publishes the official list of invasive non-native species for Santa Catarina state
Brazil	Resolution	State	151	1997	Prohibits yellow bells (<i>Tecoma stans</i>) as a noxious weed in the state

(continued)

Table 9.3 (continued)

Country	Type	Government body	Number	Year of publication	Short description
Chile	Law	Federal	19300	1994	Environmental protection law
Chile	Decree	Federal	90	1999	Regulates the importation of forestry products
Chile	Decree	Federal	53	2007	Accession to the World Organization for Animal Health and the International Plant Protection Convention of the United Nations Organization for Agriculture and Food
Chile	Resolution	Federal	1551	1998	Regulates transit of plant material
Chile	Law	Federal	Criminal law	1874	Criminal law (art. 291)
Chile	Law	Federal	20283	2008	Protection of native forests
Chile	Law	Federal	3557	1981	Prevention, control, and management of cattle diseases
Ecuador	Constitution	Federal		2008	Federal Constitution
Ecuador	Law	Federal	983	2017	Organic Code of the Environment (COA)
Ecuador	Protocol-Normative	Continental Ecuador	AM-007-2019	2019	The Ten-Year Action Plan for the prevention, management, and control of exotic species in continental Ecuador
Ecuador-Galápagos	Regulation	Galapagos	3,516	2003	Regulation of total control of species introduced of the Province of Galapagos
Ecuador-Galápagos	Decree	Galapagos	1,319	2012	Creates the Agency for Regulation and Control of Biosecurity and Quarantine for Galapagos (ABG)
Ecuador-Galápagos	Law	Galapagos	67	1998	Law of the special regime for conservation and sustainable development of the Province of Galapagos
Venezuela	Constitution	Constitution		1999	National Constitution
Venezuela	Law	Federal	5468	2000	Law of biological diversity
Venezuela	Law	Federal	39070	2008	Law of the management of biological diversity
Venezuela	Law	Federal (Orgánica)	39913	2011	Criminal Law of the Environment (Amendment of the Law of Biological Diversity)
Venezuela	Law	Federal	38946	05/06/2008	Law on Forestry and Forest Management
Venezuela	Law	Federal	40222	06/08/13	Forest Law

duty to protect the environment. The most specific regulation is the Law of management of biological diversity (year: 2008; Number: 39070), which has a chapter on the management of non-native species (Chapter IV. Articles from 75 to 81). In this chapter, the responsibilities of who controls the introduction, prioritizes, and manages non-native species at a national level are described. Environmental Criminal Law also states economic sanctions to prison terms for environmental crimes caused by the introduction of non-native species. In 2006, the National Strategy for the Conservation of Biological

Diversity was published, which includes seven strategic lines, among which the strategic line number 5 is related to non-native species: "Prevention, control and eradication of exotic species." In this strategic line, the steps for the successful management of invasive species are indicated, but methodological details to complete each step are not described.

Argentina and Chile have a more limited legal framework to tackle biological invasions compared to the other South American countries. For the most part, regulations on biological invasions in Argentina and Chile are embedded within general

environmental laws and commercial regulations (Bustos and Jacksic 2017). There is no legislation in place specifically designed to deal with biological invasions (Table 9.3). Coincidentally, these two countries also have the greatest number of non-native naturalized plant species.

9.6 Conclusions

There are thousands of naturalized invasive plants, of which, hundreds of species would qualify as being in the invasive non-native plant category in South America. Patterns of plant invasion in the continent seem to be related to habitat heterogeneity and land degradation. Also, there are legislations in place to manage invasive species (e.g., prevention, control, or eradication). However, there are immense knowledge gaps on the impacts of invasive plants. For some prominent invaders in the continent, both in terms of actual distribution and expert perception, we were unable to find a single study on their impacts in South American ecosystems or development and evaluation of management strategies. Research on biological invasions has increased in the continent over the last two decades, as well as legislation and management efforts (Zenni et al. 2016; de Andrade Frehse et al. 2016; Zenni et al. 2017; de Sa Dechoum et al. 2018), but there is clearly a long road ahead to achieve the level of knowledge and action required to reduce and mitigate impacts of biological invasions in the continent. Furthermore, the continent lacks bilateral or multilateral agreements to prevent the spread of invasive species between South American countries. Each country has been dealing with biological invasions on its own, and there is a need for greater integration across the continent.

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Biological Invasions by Plants in Continental Central America

10

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Abstract

Central American biota has been shaped by natural biological exchanges resulting from complex geological and climatic events during its formation. However, it has also been significantly affected by the arrival and spread of humans, which introduced domesticated species as well as others that incidentally came with them. Several non-native plant species have been established as a result of anthropogenic transport and the climatic and geographic properties of the region. Among naturalized species, several plants have become problematic in different ecosystems and are now recognized as invasive species. In this chapter, we present a list of non-native

species of plants for each Central American country. The plants were classified as cultivated or naturalized. From these, we have compiled some examples of plants considered invasive species. Our compilation lists 1628 non-native plant taxa (species and varieties) introduced in Central America, of which only 3.9% (64 species) are common to all countries and 50.1% (816 species) are naturalized in at least one country. We present 26 invasive plant species that are problematic in at least one or several countries. We have considered five types of natural ecosystems and two types of managed ecosystems across Central America and examined how non-native species have impacted them. Although there are invasive species in all the ecosystems analyzed, most

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of the consequences remain unknown. We conclude that many invaders have the potential to displace native plant species, significantly impact the functionality of both natural and managed ecosystems, and also have an economic impact. Policies to prevent invasions and management practices of invasive species are required among Central American countries.

Keywords

Central America · Belize, Costa Rica · El Salvador · Guatemala · Honduras · Nicaragua · Panama · Invasive plants

10.1 Introduction

Biological invasions are not a novel phenomenon in Central America. Charles Elton's seminal book on biological invasions refers broadly to the Great American Biotic Exchange as one of the most important biogeographic events of the last 60 million years. It took place after the emergence of the land bridge and the closure of the Central American canal between Middle and Late Miocene, ~13–3 million years ago (Marshall 1988; Montes et al. 2015). For the first time since the breakup of Pangaea during the Early Cretaceous Period (150–140 Ma), the biota of North and South America met once again after evolving in isolation for millions of years. This event represents one of the best-known examples of biological invasions under natural conditions. Nonetheless, this event had far-reaching consequences on the current composition of terrestrial and marine biotas (Elton 1958), not only in Central America but also in North and South America (Marshall et al. 1982; Bagley and Johnson 2014; Leigh et al. 2014). The natural faunal exchange allowed the movement and range expansion of terrestrial elements between North and South America and the isolation and diversification of marine organisms and caused physical and chemical changes in the properties of the Atlantic and Pacific Oceans (Jackson and D'Croz 1997). As a result, most of the marsupial

species of South America were driven to extinction, whereas placental mammals from North America became dominant and now comprise 50% of the present-day South American fauna. At the time of the canal closure and land bridge formation, the cold and dry conditions prevalent at the end of the last Pleistocene glaciation facilitated the interchange of temperate elements from both North and South America across the bridge. With the end of the Pleistocene glaciation ca. 10,000 years ago, strictly neotropical elements invaded the Central American tropics, and the large mammal megafauna went extinct due to increasingly warmer and humid conditions that decreased the area covered by open savannas. The “natural” invaders from both sides dispersed, preyed upon, and competed, leading to the extinction of many species, the diversification of some groups (e.g., cricetid rodents), and the overall change of communities and ecosystems (Simpson 1980; Marshall et al. 1982; Leigh et al. 2014).

The current configuration of the Central American biota is not only the result of biological exchanges, but it has also been significantly affected by the arrival of humans ca. 13,500 BP (Braje et al. 2017). Humans functioned as top predators and modified the landscape through the transportation of their associated species, including both animals and plants, in a manner similar to the now extinct megafauna (Levis et al. 2018). After humans arrived and spread throughout the continent, three migration waves brought in more species to the isthmus. The first wave resulted in the establishment of human settlements over the entire continent, including the pre-Columbian trade (Dressler 1953). The second wave comprised the arrival of and conquest by the Europeans. The third wave occurred when African slaves were forcibly resettled by the colonial powers. In all of these cases, humans have introduced domesticated species and others that incidentally came with them as a result of the global commercial trade. The crop interchange has modified the landscape and culture ever since. Nowadays, the main crops in the region are non-native species, including coffee (*Coffea arabica*), sugarcane (*Saccharum officinarum*), bananas (*Musa* spp.), rice (*Oryza sativa*), pine-

apple (*Ananas comosus*), and African oil palm (*Elaeis guineensis*). These species dominate agricultural lands and thus have significantly influenced the history and culture of Central America. Among these crops, coffee has already become invasive within forest fragments and is hard to eliminate from abandoned agricultural fields. Taken together, the establishment of invasive species is a result of anthropogenic economy due to trade and transport of agricultural goods, as well as climatic, geographic, and socioeconomic characteristics of the recipient region.

Central America is a land of contrasts regarding its climatic and geographic features. The geomorphology between the Pacific and Atlantic coasts mirrors their different geological origins (much of the Pacific rim of Central America corresponds to the subduction zone of the Cocos Plate under the Caribbean Plate) (Coates 1997). The Atlantic coast is sinuous and has an extensive continental shelf of gentle slope towards the Antilles and is separated from them by a few hundred kilometers. In contrast, the continental shelf of the Pacific coast is narrow and rounded by the Middle American Trench, reaching great depths at a short distance from the shore. The trade winds and their interaction with the intertropical convergence zone determine rainfall distribution and the overall climatic seasonality (Coates 1997; Jackson and D’Croz 1997). Temperature differences are not evident with latitude but rather vary with topography due to the interaction between wind masses (mostly Northeasterly Trade Winds) and the presence of mountain ranges in a predominantly Northeast-Southeast direction. These wind and rainfall distribution patterns have influenced the history of human colonization, as well as the location of agricultural fields. The climate of the Pacific slope is strongly seasonal with a 3–6-month-long dry season. In contrast, the Caribbean slope is humid, has a weak seasonality, and is often exposed to hurricanes and tropical storms.

The elevation ranges from 0 m.a.s.l. to the summit of the Tajumulco Volcano in Guatemala at 4220 m.a.s.l. Areas below 1000 m.a.s.l. are hot, typically reaching 30 °C. Between 1000 and 2500 m a.s.l., the average temperature ranges between 15 and 25 °C. Above 2500 m a.s.l., the

average temperature rarely reaches 20 °C, and over 3000 m a.s.l. night temperatures may fall below zero (Taylor and Alfaro 2005) (Fig. 10.1). Throughout the isthmus, an intermittent mountain range chain divides the Pacific slope from the Caribbean slope, leaving fertile valleys between the mountains. The average annual rainfall varies widely as a result of changes in topography and elevation. For instance, El Salvador, certain areas in Guatemala, Honduras, and Nicaragua show average rainfall of less than 1000 mm per year. In contrast, some other areas in Guatemala, Panama, and a large portion of Costa Rica receive large amounts of rainfall exceeding 2500 mm per year (Fig. 10.1). These contrasting weather and topographic conditions have determined the patterns of human settlement and, consequently, the use, spread, and establishment of non-native plants.

In this chapter, we have compiled a list of exotic species, which have been reviewed by specialists from Central American countries. We also reviewed the information available in previous publications and in the Global Naturalized Alien Flora database (Pyšek et al. 2017; Van Kleunen et al. 2019). When possible, we have classified the species as cultivated or naturalized. We have considered non-native species as “cultivated” if they remained cultivated in fields, parks, or gardens, whereas the ones that persist and maintain populations over multiple reproductive cycles were considered as “naturalized.” We present species as “invasive” if they were indicated as such in the respective reference; however, we only included those species that are exotic following the definition of invasive alien species of the Convention on Biological Diversity. Although the issue of invasive species has so far been neglected in the Central American region, some cases of invasive plant species are examined in the available literature, which we are reporting in this chapter. We further discuss key ecosystems in Central America that have been critically affected by invasive plants and describe the number of non-native species and their current knowledge about invasive species by country. Finally, we examine policies and strategies to control the spread and impacts of invasive species, which have been established by governments of the region.

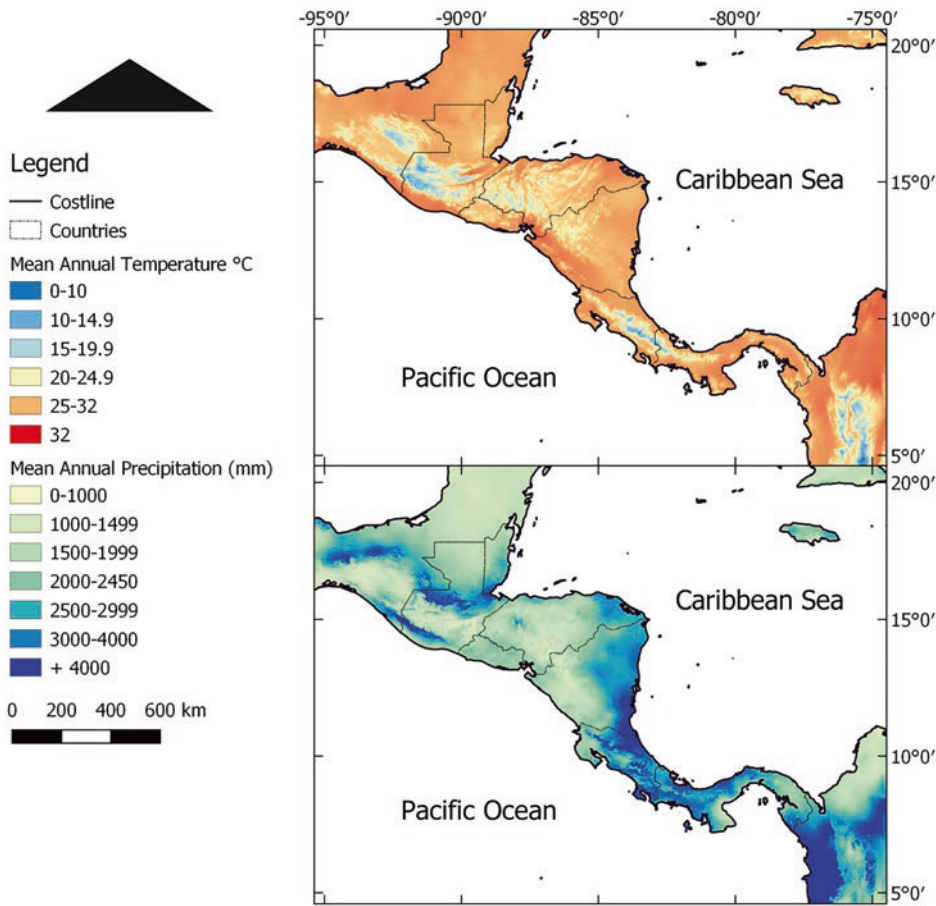


Fig. 10.1 Map of Central America with mean annual temperature and mean annual precipitation. (Data according to Hijmans et al. 2005)

10.2 Diversity by Country

The final list we compiled comprises 1555 non-native plant taxa (species and varieties) introduced in Central America (Table 10.1), classified within 178 families. Only 4.43% (69 species) of the overall list are common to all countries. A total of 678 taxa are naturalized in at least one country. However, there is no detailed information about the invasion stages of non-native species for most countries. Therefore, the previously available information on naturalized species requires a complete revision.

10.2.1 Belize

The information about the alien plant species for Belize varies according to the reference. In a specialized website of Belize's biodiversity, we found a list of 258 non-native species (Meerman 2016). The Global Naturalized Alien Flora (GloNAF) database (Van Kleunen et al. 2019) lists 61 species as naturalized (Table 10.1); however, Williams (2010) reported there are 237 alien species, but he only lists 46 species. No other reference about a particular invasive plant species was found for Belize. We considered the Meerman (2016) list with 258 non-native species to be more accurate.

Table 10.1 Diversity of the total vascular plants and naturalized species for each Central American country

Country	Continental area (Km ²)	Total vascular plant species	Total exotic species	Total naturalized species	Total invasive species	Sources
Belize	22,966	2894	258	107	11	Van Kleunen et al. (2019), Pyšek et al. (2017) and Meerman (2016)
Costa Rica	51,100	10,712	1048	280	47	Chacón and Saborío-R (2006), Avalos (2019), own data
El Salvador	21,041	2911	352	90	4	Own data
Guatemala	108,889	8681	536	300	10	CONAP (2011), own data
Honduras	112,090	5680	497	79	20	Own data
Nicaragua	130,370	7590	369	95	7	Own data
Panama	75,420	9520	373	263	8	Lopez (2012)

10.2.2 Guatemala

The Consejo Nacional de Áreas Protegidas (National Council of Protected Areas) of Guatemala elaborated a list of exotic species (CONAP 2011). We have reviewed this list and classified the species included there as naturalized or cultivated. In total, we found 536 non-native plant species, from which 300 are naturalized. The CONAP list also classified the species into three categories: species without risk (white list), species with moderate risk or without information (gray list), and species with a high risk (blacklist). In the case of plants, CONAP listed 13 species in the blacklist. Although the information about the diversity of invasive species in Guatemala is better than in other Central American countries, there is little information about specific cases of invasions (Veblen 1975; Monterroso et al. 2011; Rejmánková et al. 2018).

10.2.3 Honduras

Honduras has limited information about invasive plant species. We compiled a list of 502 non-native plants, of which we classified 79 species as naturalized and 397 as cultivated, 20 as invasive, while for 6 species, there is no information. The SENASA (Department of Plant Quarantine) proposed a list of 472 plant species commonly imported into Honduras; it includes exotic and

native plants used as ornamentals, crops, and forestry, among others (SENASA 2019). Currently, there are no assessments of the impact that alien invasive species are having on biodiversity and human well-being (DiBio 2017). The literature does not report specific invasive species cases; however, according to our perception, the number of non-native species introduced to Honduras has increased during the last three decades. Invasive species such as *Egeria densa*, *Eichhornia crassipes*, *Myriophyllum aquaticum*, and *Ottelia alismoides* are exotic aquatic plants colonizing natural areas, particularly protected areas, and threatening lagoons and lakes across the country. The rose apple (*Syzygium jambos*), the jambolan (*Syzygium cumini*), and the Ceylon blackberry (*Rubus niveus*) have been cultivated and naturalized, invading all types of forest across the country.

10.2.4 El Salvador

A preliminary revision of invasive plant species was conducted for El Salvador in 2002 (Ventura-Centeno 2002). That revision presented 50 species, including several natives, corresponding more to a list of weedy species. Our list comprised 352 non-native plant species introduced to El Salvador, of which 244 are cultivated, 90 were classified as naturalized, and 18 do not have sufficient information. More information is required on the invasion status of plant species in El

Salvador. We have detected populations of the terrestrial orchid, *Oeceoclades maculata*, growing aggressively in forest fragments in protected areas, where it has been controlled through manual removal. Another herb, *Sansevieria trifasciata*, is a very common weed within coffee plantations. Morales (2006) reported the introduced African tree *Funtumia elastica*, as naturalized after having escaped areas near La Libertad Botanical Garden. Daniel and Rodríguez (2016) also reported *Hypoestes phyllostachya*, *Thunbergia alata*, and *Thunbergia fragrans* as naturalized in secondary growth and tropical deciduous forest.

10.2.5 Nicaragua

The GloNAF database (Van Kleunen et al. 2019) reported 624 taxa as naturalized for Nicaragua. However, we suspect this number probably refers to the most common exotic (cultivated and naturalized) plants in the country. Our list includes 369 non-native species in total, from which 95 were classified as naturalized species and 274 as cultivated species. There are not many references for invasive plants in Nicaragua. There is only one study reporting two species, *Azadirachta indica* and *Spathodea campanulata*, as invasive within forestry plantations in León, Nicaragua (García-Lara 2017).

10.2.6 Costa Rica

In Costa Rica, Chacón and Saborío-R (2006) compiled a list of 1048 alien plant species. They found 22% of the species naturalized and 78% cultivated or with unknown status. A high percentage of exotic species (59%) were introduced for ornamental purposes, with continental Asia as the geographic region of origin for most of the introduced species. The plant families Poaceae, Fabaceae, and Asteraceae exhibit most species. New records have been added to the list of non-native species (e.g., Gómez-Laurito and Chacón 2008). The study of Chacón

and Saborío-R (2006) was used in an invasive species workshop, which led to the classification of 63 species as invasive (Herrera and Sierra 2005), which were included in an online database of invasive species (Chacón-Madrigal 2009a). This research was linked to the Inter-American Biodiversity Information Network (IABIN), an initiative supported by the Organization of American States (OAS). The network aimed to share information on invasive species across the Americas. Initially, several Central American countries participated in the network, but over time the network lost support, and thus, the websites and their databases are no longer available. Despite ample knowledge of biodiversity, in Costa Rica few studies have focused on invasive species (Chacón-Madrigal 2009b). Some studies have analyzed specific invasion cases (Di Stefano et al. 1998; Avalos et al. 2006; Castillo-Cruz and Rodríguez-Arrieta 2009; Morera and Granados 2013); however, more research is needed to facilitate their management and control. Many economic activities in the country facilitate the dispersion of exotic species, including the use of alien plants as ornamentals in landscaping and gardening and in agricultural operations as living fences, sources of fuel, timber and firewood.

10.2.7 Panama

Lopez (2012) analyzed an annotated plant list from Panama published by Correa et al. (2004). That list included a total of 9520 species of vascular plants for Panama, with 373 considered alien species. According to Lopez (2012), the number of alien species per region (provinces) was correlated with human population size and density. In contrast, the proportion of alien/native species was negatively correlated with forest cover. The study further identified 18 invasive species and listed 13 with the potential of becoming invasive. Other studies from Panama described specific cases of invasions by wild sugarcane and palms (Hammond 1999; Svenning 2002).

10.3 Invasive Plants by Ecosystem

We consider five types of major ecosystems (tropical dry forests, tropical rainforests, highland ecosystems, coastal lands, and wetlands) and examine how non-native species have impacted them. We also examine human-maintained ecosystems, specifically agricultural fields and tree plantations, since they have been some of the main foci for introduction of alien species, including species that later became invaders and are now causing economic and ecological problems. We present a list of the species mentioned in the next part in Table 10.2.

10.3.1 Agriculture Fields

Although weeds include both native and non-native species, the latter species commonly make up a significant portion of weeds in agricultural fields (Espinosa-García et al. 2004). Among them, grasses (Poaceae and Asteraceae) are common weeds. For instance, itchgrass (*Rottboellia cochinchinensis*) is an aggressive alien weed from Old World, common to most of the crops cultivated in Central America, including bananas, rice, sugarcane, maize, and pineapple (CABI 2019a). Each adult plant can produce up to 16,000 seeds. In the United States, itchgrass is frequently found as a contaminant in crops coming from Central America, such as beans, false coriander, flax seeds, sorghum, and turkey berry fruit (CABI 2019a). This weed causes major economic losses for farmers, who are forced to invest a significant amount of their income controlling this pest (Valverde et al. 1999). In 1992, FAO estimated that itch-grass affected more than 3.5 million ha in Central America and the Caribbean (FAO 1992). In Mexico, it is considered the most harmful weed in the country (Vibrans 1992).

The rose apple or “manzana rosa” (*Syzygium jambos*), native to the Indo-Malaysian Archipelago, was introduced to Jamaica in 1762, and from there, it got dispersed to the rest of the Neotropics as a fruiting and ornamental tree (CABI 2019b). Despite its ornamental use, the rose apple is commonly used as a shade tree and

living fence in coffee plantations. In Costa Rica, it has become an invasive species in forest fragments and secondary forests (Di Stéfano et al. 1998; Avalos et al. 2006) where it interferes with natural regeneration by creating monospecific stands. Often, it is the most frequent seedling (up to 50%) found within small secondary-forest fragments in Costa Rica; it also negatively affects the abundance of native tree species in regeneration (Avalos et al. 2006). Unfortunately, many farmers continue dispersing this species and, in some instances, use it to reforest disturbed lands.

A tall grass (3–4 height) from Asia, the wild sugarcane (“Paja Blanca” or “Paja Canalera”) (*Saccharum spontaneum*), apparently arrived by accident in the Panama Canal region before 1960 (Hammond 1999). However, a more feasible hypothesis indicates that it was deliberately introduced for the genetic improvement of sugarcane in the experimental Canal garden before 1940 (Cerezo 2010). This wild sugarcane has spread aggressively throughout agricultural fields using roads and river edges, reaching northern Costa Rica in 1992 (Palencia-Pineda 2000). About 3% of the Panama Canal Watershed is now occupied by this species (ACP and ANAM 2006). Wild sugarcane rapidly colonizes deforested lands and agricultural fields. It inhibits succession forming monospecific stands making the lands without value for agriculture or native wildlife (Hammond 1999). Different control methods, such as mowing, burning, pesticides, shading, and intensive reforestation, have been applied (Palencia-Pineda 2000). Controlled fires have been the most common method, being applied by approximately 50% of the farmers (Palencia-Pineda 2000); however, it has been demonstrated that fire facilitates its spread. Fire promotes shoot growth, which increases flowering shoot density favoring seed production. By removing leaf litter, fire gives way to newly available habitat for seedling recruitment (Saltonstall and Bonnett 2012).

Wild sugarcane crossed into Costa Rica from the Pacific Slope, and can be now found in the Caribbean region. Experimentally, it has been shown that *S. spontaneum* stems have a high sprouting capacity after drying out for up to 6 weeks (Bonnett et al. 2014). Wild sugarcane

Table 10.2 Invasive plant species mentioned in the text as problematic in Central American countries

Family	Species	Growth form	Ecosystems	Countries
Arecaceae				
	<i>Aiphanes aculeata</i>	Palm	Tropical wet forest, secondary growth	H, P
	<i>Caryota mitis</i>	Palm	Tropical wet forest, secondary growth	CR, ES, G, H
	<i>Cocos nucifera</i>	Palm	Coastlines	All CA
Bignoniaceae				
	<i>Spathodea campanulata</i>	Tree	Tropical wet forest, secondary growth, forest plantations, pastures, agriculture fields	All CA
Combretaceae				
	<i>Terminalia catappa</i>	Tree	Coastlines	All CA
Fabaceae				
	<i>Pueraria phaseoloides</i>	Vine	Tropical wet forest, secondary growth, forest plantations, pastures, agriculture fields	B, CR, H, N, P
	<i>Ulex europaeus</i>	Shrub	Pastures, disturbed areas, agriculture fields, and forest edge in highlands	CR, P
Hydrocharitaceae				
	<i>Egeria densa</i>	Herb	Wetlands	CR, ES, G, H, N
	<i>Hydrilla verticillata</i>	Herb	Wetlands	All CA
Marattiaceae				
	<i>Angiopteris evecta</i>	Fern	Tropical wet forest, secondary growth	CR
Meliaceae				
	<i>Azadirachta indica</i>	Tree	Forest plantations, secondary growth, pastures	CR, ES, G, H, N
Moraceae				
	<i>Artocarpus altilis</i>	Tree	Tropical wet forest, secondary growth	CR, ES, G, H, N, P
Musaceae				
	<i>Musa velutina</i>	Herb	Tropical wet forest, secondary growth, forest plantations, pastures, agriculture fields	CR, ES
Myrtaceae				
	<i>Syzygium jambos</i>	Tree	Agriculture fields, secondary growth	All CA
Orchidaceae				
	<i>Oeceoclades maculata</i>	Herb	Tropical dry and wet forest, secondary growth	All CA
Poaceae				
	<i>Hyparrhenia rufa</i>	Herb	Agriculture fields, pastures, savannas, tropical dry forest	All CA
	<i>Melinis minutiflora</i>	Herb	Secondary growth, forest plantations, pastures, agriculture fields in lowlands	All CA
	<i>Panicum maximum</i>	Herb	Secondary growth, forest plantations, pastures, agriculture fields in lowlands	All CA
	<i>Pennisetum clandestinum</i>	Herb	Agriculture fields and pastures in highlands	CR, G, H, N, P
	<i>Rottboellia cochinchinensis</i>	Herb	Agriculture fields, pastures, savannas	All CA
	<i>Saccharum spontaneum</i>	Herb	Pastures, disturbed areas, agriculture fields, and forest plantations	CR, P
Pontederiaceae				
	<i>Eichhornia crassipes</i>	Herb	Wetlands	All CA
Rubiaceae				
	<i>Morinda citrifolia</i>	Tree	Coastlines	All CA
Zingiberaceae				

(continued)

Table 10.2 (continued)

Family	Species	Growth form	Ecosystems	Countries
	<i>Etilingera elatior</i>	Herb	Tropical wet forest, secondary growth	CR, H, P
	<i>Hedychium coronarium</i>	Herb	Secondary growth, forest plantations, pastures, agriculture fields, and wetlands	All CA
	<i>Zingiber spectabile</i>	Herb	Tropical wet forest, secondary growth	CR, ES, H

Abbreviations: *B* Belize, *CR* Costa Rica, *ES* El Salvador, *G* Guatemala, *H* Honduras, *N* Nicaragua, *P* Panama, *CA* Central America

poses a serious economic problem to agricultural fields because of the cost and difficulties in controlling it. Some primary exportation products from Costa Rica, like pineapple, have been rejected after finding seeds of *S. spontaneum* in container trailers (Palencia-Pineda 2000). Shading out young grasses in open fields by reforesting with fast-growing trees could effectively control this very aggressive invasive species (Jones et al. 2004; Joo-Kim et al. 2008).

10.3.2 Forestry Plantations

Like many tropical countries, a substantial area in Central America is suitable and dedicated to forestry plantations. Across Central America, plantations have been established mainly in the lowlands, using native species and exotic species, such as beechwood (*Gmelina arborea*), teak (*Tectona grandis*), neem (*Azadirachta indica*), river red gum (*Eucalyptus camaldulensis*), and mangium (*Acacia mangium*), among others. Among non-native forestry plantation species, beechwood and teak occupy the highest proportion of land dedicated to forestry plantations in Central America. Teak is commonly used as living fences in silvopastoral systems. Several of these species used in forestry have become invasive and are difficult to eliminate from fields. Tree stumps of beechwood re-sprout quickly after harvest, and sometimes the seeds germinate outside plantations, persisting for a long time in abandoned plantations and their edges. The species *A. indica* has been reported as invasive in León, Nicaragua, where neem has been extensively used to reforest highly degraded lands. It grows fast and is intensively used as a source of

firewood. However, it colonizes the understory of forestry plantations of native species (García-Lara 2017), decreasing timber yield, and is particularly difficult to control. Within forestry plantations, some herbs are also common non-native weeds, such as the hairy banana (*Musa velutina*) and white garland lily (*Hedychium coronarium*); they also are invasive in forests, pastures, and wetlands (Morera and Granados 2013; Morera-Chacón 2015).

The African tulip tree (*Spathodea campanulata*) is a species with multiple uses, including ornamental, timber, living fence, and shade tree in coffee plantations. Currently, it is reported as invasive in El Salvador, Honduras, and Nicaragua (García-Lara 2017). Although the ecological impact of this species has not been adequately measured, there is evidence showing that it could significantly impact populations of native bees in Costa Rica. The nectar of *S. campanulata* contains toxic alkaloids capable of killing native bees and birds (Trigo and dos Santos 2005). Jiménez (2008) explored 692 flowers of *S. campanulata* in Costa Rica and found more than 200 dead stingless bees belonging to 14 different species. The spread of this species in coffee plantations could significantly impact coffee productivity by decreasing bee populations and related coffee pollinators.

10.3.3 Tropical Dry Forests

In Central America, tropical dry forests are found along the Pacific slope, which also has the highest concentration of human settlement. They once covered 20% of Central America, but today most of the original area has been converted into agri-

culture fields, grasslands, savanna, or cities (Portillo-Quintero and Sánchez-Azofeifa 2010). It is estimated that only 2% of the original tropical dry forest remains in small isolated patches. Although it was initially harvested for timber, most of the transformation in the last century (1930–1970) occurred when the dry forest was converted to human-maintained pastures (Griscom and Ashton 2011). The grasses used for livestock were mainly exotic species introduced from Africa. At least three species have been intensively used as pastures: guinea grass (*Panicum maximum*), molasses grass (*Melinis minutiflora*), and jaragua (*Hyparrhenia rufa*). Guinea grass was first reported in the Lesser Antilles in the seventeenth century and reached Central America in the mid-nineteenth century. The introduction of molasses grass is less documented; however, it probably arrived in America early in the nineteenth century and was first reported in Central America (Costa Rica) in 1908. The jaragua arrived late to Central America compared to other African grasses, and it was first reported in Costa Rica in 1920 (Parsons 1972).

The cattle-ranching industry based on the use of extensive areas cultivated with African grasses reached its maximum development in Guanacaste (Costa Rica) and Nicaragua in the late 1960s and 1970s. In these countries, jaragua is the most common pasture grass, and it has invaded savannas and forests and has created a barrier for forest restoration when pastures were abandoned after meat prices fell in the 1980s. Jaragua grass has demonstrated a high capacity to outcompete native grasses, preventing germination and establishment of native seedlings while increasing the frequency and intensity of fires and halting succession (Janzen and Hallwachs 2016). It forms tall and dense stands (1–2 m), decreasing the light reaching the soil in the wet season and crushing natural regeneration when it dries in the dry season (Griscom et al. 2009). At the ecosystem level, grasses can also alter the productivity or trophic structure, the microclimate conditions, sunlight interception, water and nutrients availability, and competitive interactions, all of which compromise ecosystem stability (Williams and Baruch 2000).

Furthermore, the African orchid (*Oeceoclades maculata*) represents a particular case among invasive plants in Central America. Firstly, orchids rarely are considered as invasive species at the global scale (Pyšek et al. 2017). Secondly, it is invasive both in tropical dry forests and in tropical wet forest across the neotropics (Kolanowska 2014). Thirdly, only few herb species are invasive in the understory of tropical forests.

10.3.4 Tropical Wet Forests

Tropical forests with high diversity, like tropical rainforests, have high biotic resistance and are rarely invaded by plants (Martin et al. 2009). However, it is not always what we observe in the field. For instance, in Gamboa, Panama, eight palm species (*Aiphanes aculeata*, *Areca triandra*, *Bentinckia nicobarica*, *Dypsis madagascariensis*, *Livistona saribus*, *Ptychosperma macarthurii*, *Roystonea oleracea*, *Roystonea regia*) have been reported as naturalized (Svenning 2002). Other four palm species (*Caryota mitis*, *Palandra aequatorialis*, *Pigafetta filaria*, and *Pinanga kuhlii*) (OET 2012) have been reported as problematic in Las Cruces, Costa Rica. In both places, the invasive plants escaped from botanical gardens introducing species as ornamentals. Indeed, ornamental plants are frequently naturalized in the tropical rainforest. For instance, several exotic species of gingers, such as the ginger wort (*Zingiber spectabile*) or the torch ginger (*Etilingera elatior*), are abundant within the forest or along the forest edge at sites near botanical gardens or experimental agricultural stations in Costa Rica (Fernández 2008; OET 2012). In the Wilson Botanical Garden in Costa Rica, a giant fern from Australasia (*Angiopteris evecta*) with fronds measuring up to 9 m has naturalized in the forest fragments close to the garden. Although the invasion of this fern is incipient, it has the potential to colonize more sites in Central America, as it has been predicted by models (Christenhusz and Toivonen 2008).

The introduction of fodder plants also might facilitate invasive species to colonize tropical

rainforest. For example, the tropical kudzu (*Pueraria phaseoloides*) is a vine widely introduced as fodder in almost all Central American countries. It has propagated quickly, and it is common in forests along rivers, forest edges, pastures, and secondary growth. The effect of kudzu on the ecosystems is still unknown; however, in Mexico, it has been considered as a species with the potential to have a high impact in agricultural fields according to an assessment of introduced legumes (Sánchez Blanco et al. 2012).

Within tropical wet forests, trees naturalize less frequently than palms, herbs, or vines. However, increasing populations of breadfruit (*Artocarpus altilis*) have been observed in the wet forest in the southern Pacific region of Costa Rica. In secondary regrowth sites along riparian habitats, densities of 1053 trees/ha have been registered (ECM, unpublished data). The effect of breadfruit tree on forest ecosystems is still unknown and thus merits further investigation.

10.3.5 Highlands

In one of the oldest references of alien species for Central America, Veblen (1975) compared the invasive species between the Guatemala highlands and California. He reported 68 alien species in the highlands of Guatemala. Among the species reported, he mentioned kikuyu grass (*Pennisetum clandestinum*), which commonly occurs along roadsides (Veblen 1975). In Costa Rica, the kikuyu grass was introduced about 1928 on the slopes of Irazú Volcano; it outcompetes other native grasses and is considered as a pest. After the eruptions of Irazú Volcano (1964–1965), kikuyu grass was favored by ash and the absence of the other grasses, which were removed by volcanic eruptions (Parsons 1972). Nowadays, it still is very common in the mountains in Costa Rica.

Many species reported by Veblen (1975) in the highlands of Guatemala are native to Europe. Similarly, Bernhardt and Koch (1994) found many European weeds in the highlands of Costa Rica. This is not a mere coincidence but seems to result from the fact that the climate of the Central American highlands was more familiar to

European settlers than the hot and humid climate in lowland regions. The Europeans introduced crops and plants to support livestock, which was also introduced very early after arriving to America. Many weeds also came with the “new” crops and established in the middle elevations and highlands. For instance, gorse (*Ulex europaeus*), an invasive species elsewhere, grows in the forest edge and pastures in the highlands of the Poás and Barva volcanoes in Costa Rica (Standley 1937). Intriguingly, unlike in many other regions of the world, gorse did not become as invasive in Central America, where it has been reported for more than 85 years and populations seem to be stable in recent years (CABI 2019c).

10.3.6 Coastal Ecosystems

Two exotic species have dramatically changed the landscape of the coastlines along Central America in such a way that they became intertwined with the culture. Nowadays, it is difficult to imagine Central American beaches without them: the coconut tree (*Cocos nucifera*) and the Indian almond tree (*Terminalia catappa*) (Harries 1978). The two species were introduced very soon after contact with Europeans. We will never know the impacts of these two species in coastal ecosystems because they are found everywhere, although the effect of coconuts on communities and ecosystems has been long established (Young et al. 2017). More recently, the great morinda (*Morinda citrifolia*) has also become very frequent in the Caribbean, probably introduced due to the use of seeds in traditional medicine.

10.3.7 Wetlands

Ellison (2004) estimated that wetlands in Central America cover ca. 40,000 km² (~8%) of the land area. Wetlands include several aquatic ecosystems such as lakes, rivers, estuaries, and artificial reservoirs. Although Ellison (2004) made a complete revision of environmental issues of wetlands, invasive species were only briefly described. Aquatic plants tend to have widespread distributions and

long-distance dispersal mechanisms, and sometimes they are difficult to classify as exotic due to their natural range extensions. Several native species have been classified as “invasive” because their populations have increased dramatically after disturbances. For instance, in Costa Rica, southern cattail (*Typha domingensis*) increased in coverage from below 5% to over 95% in the Palo Verde marsh after cattle removal (McCoy and Rodríguez 1994). Moreover, the pantropical golden leather fern (*Acrostichum aureum*) has been considered an invasive species because it thrives after the mangrove is disturbed. In both cases, the two native species were favored by alterations in the ecosystems. Other exotic species have invaded wetlands in several Central American countries, and they have become problematic. Water thyme (*Hydrilla verticillata*) is an aquatic plant from the Old World, which is naturalized in all Central American countries. The invasion of this plant has been studied in the Lake Izabal and Lake Atitlán in Guatemala (Binimelis et al. 2007; Barrientos and Allen 2008; Monterroso et al. 2011; Rejmánková et al. 2018) and in ponds on pastures in Costa Rica (Haider et al. 2016). In Guatemala, the presence of water thyme has been suggested to impact fisheries, recreation, and tourism by hindering the movement of boats and reducing the aesthetic value of the lake. Several studies have focused on the impact of water thyme on fish communities, although the results have been equivocal (Arrivillaga 2003; Barrientos and Allen 2008). Other species, such as large-flowered waterweed (*Egeria densa*) and common water hyacinth (*Eichhornia crassipes*) are abundant in lakes, reservoirs, rivers, estuaries, and other wetlands. Water hyacinth causes physical interference with navigation and fishing and reduces water volume of reservoirs during the dry season (CABI 2019d).

10.4 Policies and Management

In general, the issue of invasive species has been neglected by governmental offices in Central America, although some initiatives have been launched to prevent the uncontrolled spread of invasive species (e.g., CONAP 2011). Such efforts

are promoted to enforce the goals of the Convention on Biological Diversity or by monitoring very problematic invasive species (e.g., *Saccharum spontaneum* in Panama or *Hydrilla verticillata* in Guatemala) in Central American countries. However, this is mainly since some invasive species are weeds in agricultural fields, but management practices are rarely implemented in natural areas. Although specific biosecurity policies to prevent the arrival of invasive species do exist, the implementation of those regulations is weak (Allen et al. 2017). Universities and NGOs should give more support to initiatives focused on preventing and controlling invasive species and educating people about the issue. For instance, botanical gardens are fundamental for the conservation of biodiversity, management strategies and the education of the general public; however, they have also become focal points for the dispersal of exotic species (e.g., Svenning 2002; OET 2012). If not managed well, plant collections can favor the dispersal of introduced species with the potential to become invasive. Some entities keeping live plant collections include botanical gardens, urban planning companies keeping nurseries to establish gardens, hotels maintaining arboretums, and universities and educational institutions maintaining plant collections. More recently, the commercialization of genetic material also takes place over the Internet, through the sale of seeds and other propagules (Chacón-Madrigal 2009b). So far, quarantines, customs control and internal regulations for the management of diversity are weak or nonexistent. Even when control policies do exist, they are difficult to enforce. Given this scenario, the most practical solution should be to educate the general public about the risks of spreading non-native species. It might be illusory to expect that there will be greater control of the dispersion of alien species through implementation of laws or regulations in the short term. However, in order to obtain the attention of governmental agencies, it will be necessary to quantify the economic costs of plant invasions for local economies. Therefore, it is crucial to generate research aiming to understand the impact of exotic plants on natural and managed ecosystems.

10.5 Conclusions

The last report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (Díaz et al. 2019) lists invasive species as one of the five most important drivers of biodiversity loss and associated loss of ecosystem function. The report also alerts about the destruction of the ecosystem functionality by climate change and asks for immediate and significant action from all governments to slow down its catastrophic consequences. Therefore, an important recommendation from that report is the request to identify and prioritize invasive alien species within all signatory countries. However, as the general tendency is a continuous increase of naturalized plants (Van Kleunen et al. 2015), stronger and firm actions need to be taken to monitor this trend. Despite preliminary efforts to elaborate lists of exotic plants in Central American countries, there has been no consistent report.

Central America is one of the world regions most seriously impacted by climate change, so that a baseline must be generated to measure the negative aspects of invasive plant species. Although most of the consequences remain unknown, many invasive plants could replace native plant species, which have been displaced by climate change but have been carrying out crucial ecosystem functions. Universities and NGOs should be involved in invasive plant research, to gather the crucial knowledge that could be used to derive conservation and management policies in compliance with governmental offices. Considering the significant effects of invading organisms on biodiversity, the functionality of the natural and managed ecosystems, and the economic impact that they generate, their registration is not only of scientific importance but also of economic relevance. The data presented in this chapter should serve as a starting point for analysis, aiming to explore these aspects and fill some of the information gaps that currently exist regarding the impacts of invasive plants on Central American ecosystems.

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Plant Invasions in Africa

11

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Abstract

This chapter reviews the current status of invasions of non-native plants in Africa. It draws on the most comprehensive global database of naturalized plant species (GloNAF) to provide a quantitative assessment of the distribution of naturalized plants across the continent. South Africa has the greatest number of naturalized

plant species of any African country (1139), and another 7 countries have more than 300 naturalized species. The number of naturalized plant species is strongly positively correlated with native plant species richness. Equatorial regions harbour fewer naturalized species than temperate regions, and regions with Mediterranean-type climate have more naturalized species than tropical and subtropi-

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cal regions. Patterns for naturalized species from GloNAF do not reflect the distribution of non-native species that invade and transform natural and semi-natural ecosystems. Quantitative data on such invasive species were available only for South Africa. The situation for the whole continent was assessed using published and unpublished resources, the experience of the authors and correspondence with regional experts. Distribution patterns are discussed, a preliminary list of the 20 most widespread and impactful invaders of natural ecosystems was compiled, and information was collated on their impacts and the attempts to manage these invasions. Many invasive plants have substantial impacts on biodiversity and ecosystem services and have major negative effects on human livelihoods. Such impacts have only been quantified for a handful of species and a few regions. South Africa is the only African country that has invested in substantial and systematic efforts to manage plant invasions. Examples of approaches for managing plant invasions and the barriers to success are discussed. There is an urgent need for standardized assessments of the extent and impacts of plant invasions across Africa. Such information is crucial for informing policy and justifying the allocation of resources to management. Suggestions are provided on key changes needed to improve the effectiveness of management of plant invasions at the regional level in Africa.

Keywords

Biological invasions · GloNAF · Impacts · Inventory · Management · Plant invasions · Tree invasions

11.1 Introduction

Africa is the world's second largest and second most populous continent. The African mainland and its adjacent islands cover about 30.3 million km², 6% of the Earth's total surface area and 20% of its land area. In 2019 the continent was home to about 1.3 billion people, 17% of the world's

human population. Africa, including Madagascar and several archipelagos, contains 54 fully recognised sovereign states (countries), 9 territories and 2 independent states with disputed sovereignty (there are 55 member states in the African Union). About two-thirds of Africa's land area and 32 (59%) of its countries occur mainly in the Northern Hemisphere. Around 80% of the continent lies within the band 30 degrees on either side of the equator.

Africa has the most phylogenetically diverse flora of any continent, although it is not the richest in species (White 1983). Much of the continent's floristic diversity can be attributed to the fact that five of the world's ten principal climate types defined by Walter and Lieth (1960–1967) occur in Africa, namely: (1) equatorial type, humid or with two rainy seasons; (2) tropical type with summer rain; (3) subtropical type, hot and arid; (4) Mediterranean type, with arid summer and winter rain, frost rare; and (5) mountain types. White (1983) recognized 16 main vegetation types (“formations”) in Africa. These include (1) formations of regional extent (forest, woodland, bushland and thicket, shrubland, grassland, wooded grassland, desert and Afroalpine vegetation); 2) formations intermediate between those belonging to group 1 and mostly of restricted distribution (scrub forest, transition woodland, scrub woodland); (3) edaphic formations of distinct physiognomy (mangrove, herbaceous freshwater swamp and aquatic vegetation, halophytic vegetation); (4) formations of distinct physiognomy, but restricted distribution (bamboo); and (5) unnatural vegetation (anthropic landscapes).

Scientific contributions on biological invasions from Africa are markedly under-represented in the global literature in general (Pyšek et al. 2008), and apart from South Africa (e.g. Richardson et al. 1997, 2020b for reviews), this is certainly also the case for plant invasions (Richardson and Rejmánek 2011; Rejmánek and Richardson 2013; Turbelin et al. 2016; CABI 2020; ISSG 2015). Despite the under-representation of Africa in publications on plant invasions, many regions of the continent face huge problems with invasive plants (de Wit et al. 2001; de Groote et al. 2003; Maundu et al. 2009; Shanungu 2009; Borokini 2011; Kebede and

Coppock 2015; Shackleton et al. 2017a, b, c, d; Witt and Luke 2017; Witt et al. 2020a, b; Richardson et al. 2020b). Socio-economic problems associated with the impacts caused by plant invasions are escalating rapidly throughout the continent (Boy and Witt 2013).

This chapter presents an assessment of the status of plant invasions in Africa. It draws on a global database of naturalized and invasive non-native plants, peer-reviewed literature, grey literature and several reliable Internet sources, our own experiences and unpublished records and correspondence with other researchers. The concepts of “non-native”, “naturalized”, “invasive” and “transformers” in this chapter follow the definitions proposed by Richardson et al. (2000b).

Efforts devoted to recording the distribution, status, abundance and impacts of non-native plant taxa have been very uneven across Africa. South Africa has been well surveyed for non-native species, and there is a rich literature on all aspects of plant invasion science (e.g. Richardson et al. 2000a; Henderson and Wilson 2017; van Wilgen et al. 2020). Several recent publications have greatly improved our knowledge of the distribution, abundance and impacts of invasive plants in eastern Africa (Lusweti et al. 2011; Witt and Luke 2017; Witt et al. 2018). National or regional syntheses of naturalized and invasive plant species have been undertaken for Algeria (Meddour et al. 2020), Angola (Rejmánek et al. 2017), Chad (Brundu and Camarda 2004), Ghana (Ansong et al. 2019), Lesotho (Kobisi et al. 2019), Libya (Mahklouf 2020), Madagascar (Binggeli 2003; Kull et al. 2012), Namibia (Brown et al. 1985; Bethune et al. 2004), Eswatini (formerly Swaziland; SNTC 2016), Sudan and Southern Sudan (Omer et al. 2021) and Zimbabwe (Maroyi 2006, 2012, 2017). Other lists focus on specific areas [e.g. Dawson et al. 2008 and Sheil 2008 for the Usambara Mountains, Tanzania; Rejmánek 1996 and IUCN/PACO 2013 for protected areas in Uganda and West Africa; and Akodéwou et al. 2019 for the Togodo Protected Area in southeastern Togo] or focus mainly on agricultural weeds, many of which are non-native species [e.g. Bogdan 1950, 1965; Ivens 1967; Terry 1984; Terry and Michieka 1987 for East

Africa; Germain 1952; Mullenders 1954; Schmitz 1971; Mosango 1983a, b; Lubini 1986 for Central Africa; Wild 1955; Drummond 1984 for Zimbabwe; and El Hadidi et al. 1996 for Egypt].

Other publications have appeared on single species or groups (genera or families) of invasive plants or functional groups of species that provide important information on distribution patterns, ecological aspects, impacts and management initiatives in parts of Africa. Examples are Cactaceae (Novoa et al. 2015, 2019); *Casuarina* species (Potgieter et al. 2014); *Opuntia stricta* (Foxcroft et al. 2004; Shackleton et al. 2017d); *Chromolaena odorata* (Shackleton et al. 2017c); *Lantana camara* (Bhagwat et al. 2012; Vardien et al. 2012; Shackleton et al. 2017b; Agaldo 2020); *Tithonia* species (Witt et al. 2019); *Eucalyptus* species (Rejmánek and Richardson 2011); Pinaceae and other conifers (Richardson and Rejmánek 2004); *Prosopis* species (Shackleton et al. 2014; Kebede and Coppock 2015; Mbaabu et al. 2019); trees and shrubs (Richardson and Rejmánek 2011); *Mimosa pigra* (Shanungu 2009; Witt et al. 2020a); *Mimosa diplotricha* (Witt et al. 2020b); and bamboos (Canavan et al. 2017).

There have also been several reviews of invasive plants in protected areas (e.g. Foxcroft et al. 2010, 2013, 2017; Witt et al. 2017; Shackleton et al. 2020a, b), invasions associated with the use of non-native trees in agroforestry (Richardson et al. 2004; see also Kull et al. 2011) and invasions of non-native trees in urban areas (Potgieter et al. 2017). These sources provide useful insights on the status and trends of plant invasions and on challenges for management in Africa.

We used the most comprehensive global database of naturalized plants along with collated and summarized available information on invasions in natural and semi-natural ecosystems from published sources and unpublished records to provide a preliminary overview of plant invasions in Africa. We also review what is known of the impacts of plant invasions and the approaches taken to manage plant invaders in different parts of the continent. We then discuss recent efforts to improve the knowledge of plant invasions and conclude with suggestions on priorities for

research to improve the understanding of invasions across the continent.

11.2 Methods

The Global Naturalized Alien Flora (GloNAF) database (version 1.1; 2015) contains inventories of naturalized non-native plant species for 843 regions worldwide (e.g. countries, states, provinces, districts, islands; van Kleunen et al. 2015, 2019; Pyšek et al. 2017). The database is a reviewed compilation of national and subnational lists of naturalized non-native plant species that are published or unpublished or developed specifically for GloNAF, e.g. for the provinces of China, Ghana and the states of India (Inderjit et al. 2018; Ansong et al. 2019). The data are collected in a standard way that allows for comparisons among individual regions and taxonomic groups in a robust way (e.g. Canavan et al. 2019). Besides the assignment to continents, each GloNAF region is assigned to one of the following zonobiomes, a classification system of zonal vegetation distributed according to macroclimate: I. Tropical (equatorial); II. Tropical (savanna); III. Subtropical (arid); IV. Mediterranean; V. Warm temperate; VI. Temperate (nemoral); VII. Arid temperate (continental); VIII. Cold temperate (boreal); and IX. Arctic (based on Walter and Breckle 1991; see details on invasions in these units in Pyšek et al. 2017).

Data from GloNAF provide the best available objective assessment of naturalized plant species in Africa. However, the data do not reflect the status of invasive plants that cause major damage in natural and semi-natural ecosystems (“transformers” sensu Richardson et al. 2000b). The status of such invasive plant species has only been assessed objectively for South Africa; for the rest of the continent, we relied on a review of published information (sparse for most of the continent) using standard databases (see discussion in Sect. 11.4) and search engines and on the insights of invasions in many African countries of the authors (especially ABRW) to compile a preliminary account.

Data on species numbers were analysed to reveal information on the patterns across different zonobiomes and mainland/island regions. In the study area, we recorded only four zonobiomes (temperate, arid, tropical and subtropical). The analyses were based on analyses of covariance followed by deletion tests that identify the most parsimonious models. Data on the extent of regions was log-transformed. Normal distribution of residuals was visually checked. All calculations were made in R (3.6.2).

We reviewed the current state of knowledge of impacts and management of invasive plants using Google Scholar, Web of Science, other online resources, research libraries at our own institutions and correspondence with researchers and managers throughout Africa.

11.3 Results

11.3.1 Continental Patterns of Africa's Naturalized Plants: A Quantitative Analysis

The number of naturalized non-native species reported from African countries (for which data are available in the GloNAF database; van Kleunen et al. 2015, Pyšek et al. 2017) is shown in Table 11.1. South Africa has the largest number of recorded naturalized species (1139), but 7 other countries also harbour more than 300 such species: Democratic Republic of the Congo 522, Madagascar 517, Ethiopia 421, Morocco 410, Benin 333, Algeria 328 and Eswatini 315. Because of its extremely rich native flora, the contribution of naturalized non-natives to the total floristic richness of South Africa is rather low: only 4.8%. The countries that rank highest in this respect in GloNAF are Chad (11.6%), Benin (11.4%) and Eswatini (10.4%); only those three exceed 10% (Table 11.1). South Africa is also richest in terms of number of invasive species (for species placed in this category in GloNAF), but this is probably more a reflection of the lack of a standard classification scheme for non-native floras in African countries rather than

Table 11.1 Numbers of naturalized, percentage of naturalized taxa in the whole flora, invasive and native species in African countries as recorded in GloNAF database

Country	Naturalized no.	Naturalized%	Invasives no.	Native no.
Algeria	328	7.7	38	3953
Angola	227	4.2	2	5185
Benin	333	11.4	9	2584
Botswana	170	5.3	51	3041
Burkina Faso	149	7.2	6	1918
Burundi	187	6.0	2	2909
Cameroon	296	3.6	10	7850
Central African Republic	57	1.6	2	3602
Chad	274	11.6	6	2080
Congo	56	1.2	8	4538
Cote d'Ivoire	266	6.5	9	3853
Democratic Republic of the Congo	522	4.5	10	11,007
Djibouti	42	6.1	1	641
Egypt	179	8.7	33	1890
Equatorial Guinea	187	5.4	1	3250
Eritrea	65	8.5	6	700
Eswatini (Swaziland)	315	10.4	10	2715
Ethiopia	421	6.0	16	6603
Gabon	94	1.4	2	6651
Gambia	11	1.1	5	974
Ghana ^a	291	8.9	25	2974
Guinea	86	2.8	8	3007
Guinea Bissau	97	6.2	3	1459
Kenya	145	2.2	39	6506
Lesotho	206	6.4	2	3000
Liberia	141	6.0	4	2200
Libya	147	7.5	2	1825
Madagascar	517	4.1	101	12,000
Malawi	50	1.3	9	3765
Mali	74	4.1	7	1741
Mauritania	84	7.5	3	1040
Morocco	410	8.0	8	4700
Mozambique	103	1.8	25	5692
Namibia	218	4.8	58	4300
Niger	37	2.5	7	1460
Nigeria	193	3.9	19	4715
Rwanda	229	8.4	6	2500
Senegal	97	3.7	9	2500
Sierra Leone	76	3.5	2	2090
Somalia	63	2.0	5	3028
South Africa ^b	1139	4.8	374	21,643
Sudan	59	1.8	9	3156
Tanzania	157	1.5	28	10,008
Togo	63	2.1	3	3003
Tunisia	225	5.9	8	3573
Uganda	152	3.0	25	4848
Zambia	84	1.3	13	6280
Zimbabwe	238	3.9	27	5930

van Kleunen et al. (2019), Pyšek et al. (2017) - details of data sources are provided in these publications

^aUpdated from Ansong et al. (2019)

^bUpdated from Pyšek et al. (2020)

the real situation. The spatial distribution of naturalized species richness is shown in Fig. 11.1.

The number of naturalized species on African islands increases with region area that explains 61% of the variation (Fig. 11.2a). The lack of a significant species-area relationship for mainland regions is partly due to the effect of other factors such as climate, as manifested through zonobiomes (see below); individual zonobiomes harbour regions of different sizes that may disrupt the relationship. There is a strong and highly significant positive relationship between the numbers of naturalized and native plant species across Africa, and this relationship holds true for both islands and mainland regions. However, the intercepts of the relationships are different, suggesting higher susceptibility of islands to invasion; for the same number of native species, islands harbour

more naturalized non-natives (Fig. 11.2b). Finally, there is a distinct and highly significant effect of latitude on naturalized species richness which explains 33% of variation in the data, with equatorial regions harbouring fewer naturalized species (Fig. 11.2c). The trend remains significant for levels of invasion of mainland regions ($F = 10.2$, $df\ 2,47$, $p < 0.001$) (measured as naturalized non-native species as a percentage of native plus naturalized species, therefore accounting for different sizes of particular regions).

There is an effect of zonobiome on naturalized non-native species richness in Africa. Regions with Mediterranean-type climates have significantly more naturalized species (measured as an average number of naturalized species per region) than tropical and subtropical regions. The high levels of naturalization in temperate regions are

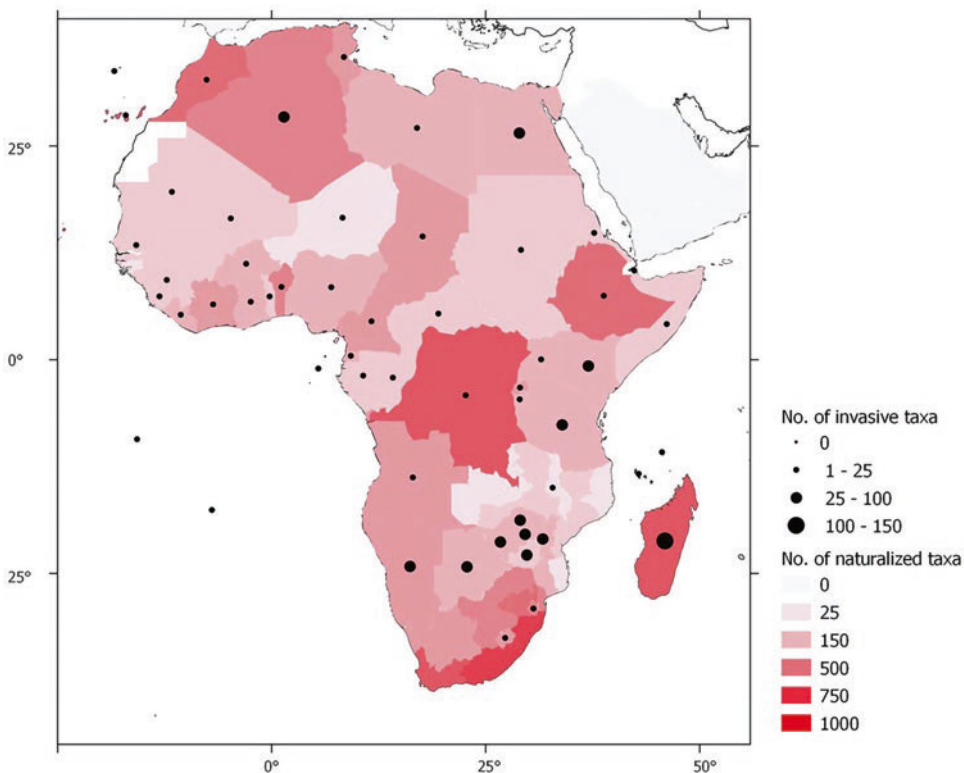


Fig. 11.1 The richness of naturalized and invasive plant taxa in African countries based on records in GloNAF. The numbers of naturalized species are shown by shading intensity, those of invasive species by the size of the sym-

bol. (Based on data from Pyšek et al. 2017). Note that the colour scale is continuous; colours associated with the species numbers in the legend do not refer to discrete categories but to the thresholds of 0, 25, 150, 500, 750 and 1000 species

explained by high levels of invasions on islands north of Africa (Fig. 11.3). However, in terms of total number of naturalized species occurring in a zoniome, the pattern is reversed, and tropical mainland areas have more naturalized species across regions than areas with Mediterranean-

type climate (1193 vs. 990). The same pattern, though less pronounced, holds for islands with tropical climate which have more naturalized species than those with temperate climates (1598 vs. 1297). This is because tropical regions harbour large numbers of naturalized species which have

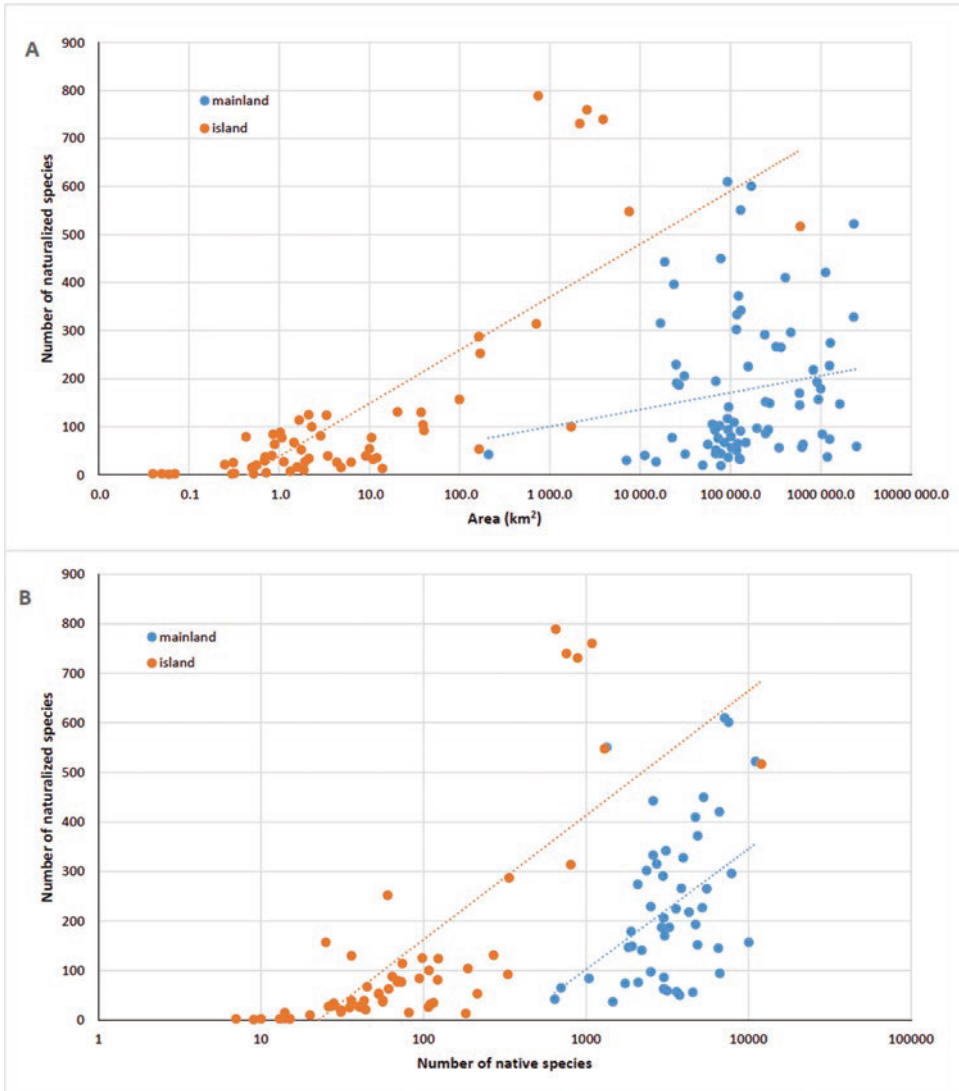


Fig. 11.2 Relationship between numbers of naturalized species in African regions and region size, between naturalized and native species and latitudinal trends in numbers of naturalized species. (a) The slopes for mainland and islands are significantly different (deletion test: $F = 8.206$, $df = 132, 133$, $p = 0.005$; the slope of 110.56 for islands is significantly different from zero: $F = 90.17$, $df = 1, 57$, $p < 0.001$, $R^2 = 0.61$; for mainland it is not: $F = 1.973$,

$df = 1, 75$, $p = 0.164$). (b) The slopes for mainland and island are not significantly different (deletion test: $F = 0.0067$, $df = 104, 105$, $p = 0.935$); the common slope of 108.52 is different from zero: $F = 47.06$, $df = 1106$, $p < 0.001$). (c) The model for data pooled across mainland and island: $F = 32.15$, $df = 2133$, $p < 0.001$. (Data based on non-overlapping regions as shown in Pyšek et al. 2017)

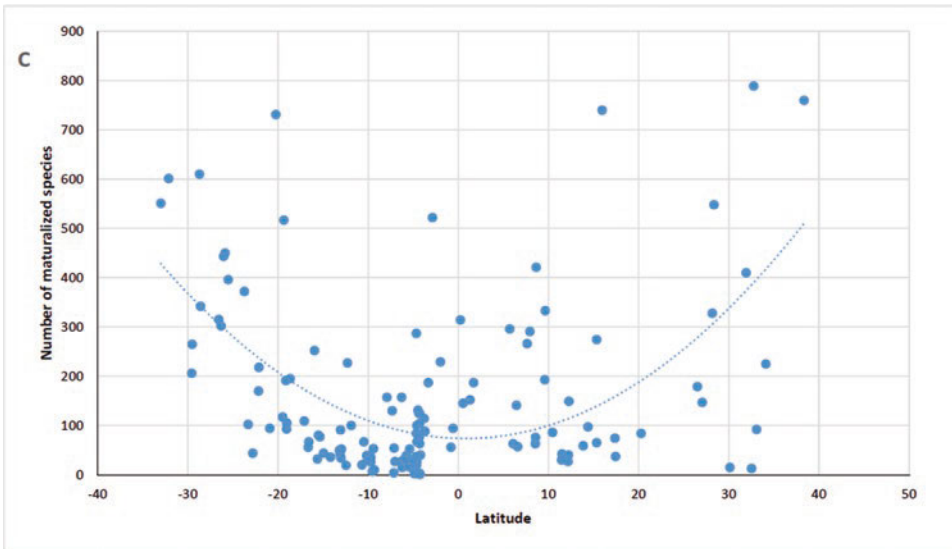


Fig. 11.2 (continued)

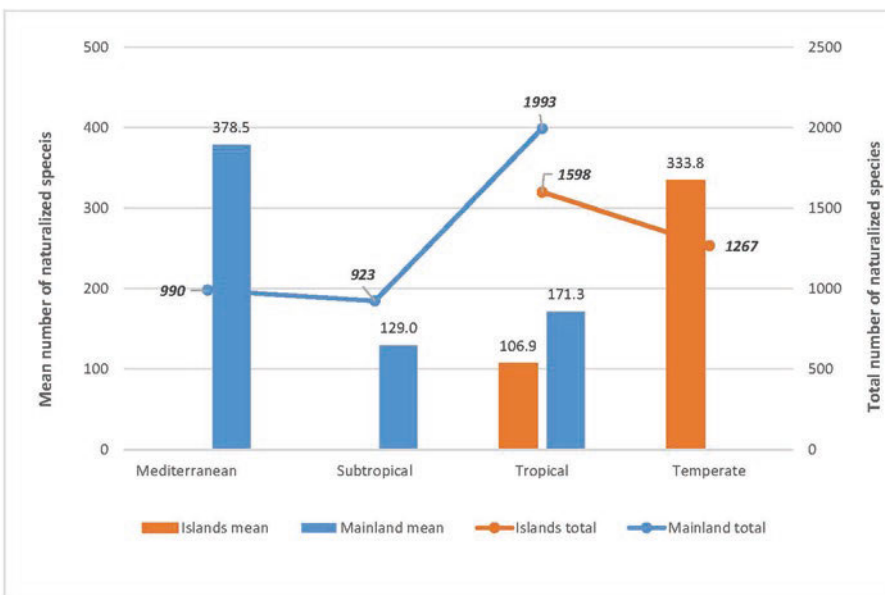


Fig. 11.3 Distribution of naturalized species in African regions by zoniomes, shown separately for the mainland and islands. Data are for mean number of species per region and the total number of species in a zoniome (bold italics). There are significant differences in mean numbers of naturalized species among regions (merged for mainland and islands) located in different zoniomes

(one-way ANOVA, $F = 4.629$, $df = 3132$, $p < 0.01$). This is due to significant ($p < 0.05$) differences between subtropical vs. Mediterranean and tropical vs. Mediterranean zones and marginally significant differences between temperate and subtropical ($p < 0.1$) and tropical vs. temperate ($p < 0.06$) zones. (Source: GloNAF database, Pyšek et al. 2017)

usually small ranges, which means that they occur, on average, in fewer regions – the opposite pattern to areas with Mediterranean-type climates

where individual naturalized species are more frequent in terms of regional occurrences (Fig. 11.3).

Bidens pilosa (occurring in 61% of all regions), *Ricinus communis* (60%), *Senna occidentalis* (60%), *Catharanthus roseus* (56%) and *Euphorbia hirta* (54%) are the most widely naturalized non-native plant species across all African regions and are reported from more than half of the regions. In total, 32 species occur in more than one third of all regions (Table 11.2). Some of the naturalized species are more often recorded on islands than on mainland; these include many economically utilized species, e.g. *Phyllanthus amaris*, with 69% of its records on islands, *Carica papaya* (67%) and *Agave sisalana* (62%). Other spe-

cies with more than half of their occurrence records on islands are *Leucaena leucocephala*, *Datura metel*, *Cyanthillium cinereum* and *E. hirta*. This pattern is even more pronounced considering that there were more mainland than island regions in the data set (77 vs. 59). In contrast, *Acanthospermum hispidum* (only 2% of records on islands), *S. obtusifolia* (4%), *Eclipta prostrata* (7%) and *Amaranthus spinosus* (8%) occur almost exclusively on the African mainland. Perennials (42% of the 32 shown in Table 11.2), annuals (30%) and trees (14%) are the best represented life forms; other life forms are less frequent, with three shrubs

Table 11.2 Numbers of regions in Africa occupied by naturalized plant species based on records in the GloNAF database (Pyšek et al. 2017)

Species	Family	Life history	Mainland	Island	Total
<i>Bidens pilosa</i>	Asteraceae	Annual	62	21	83
<i>Ricinus communis</i>	Euphorbiaceae	Perennial	52	29	81
<i>Senna occidentalis</i>	Fabaceae	Annual	47	30	77
<i>Catharanthus roseus</i>	Apocynaceae	Perennial, shrub	37	39	76
<i>Euphorbia hirta</i>	Euphorbiaceae	Annual	34	40	74
<i>Alternanthera sessilis</i>	Amaranthaceae	Aquatic, perennial	54	12	66
<i>Lantana camara</i>	Verbenaceae	Shrub	44	20	64
<i>Ageratum conyzoides</i>	Asteraceae	Annual	51	11	62
<i>Euphorbia prostrata</i>	Euphorbiaceae	Annual	31	30	61
<i>Oxalis corniculata</i>	Oxalidaceae	Annual, perennial	45	16	61
<i>Cyanthillium cinereum</i>	Asteraceae	Annual	28	32	60
<i>Solanum americanum</i>	Solanaceae	Annual, perennial	31	27	58
<i>Portulaca oleracea</i>	Portulacaceae	Annual, succulent	50	6	56
<i>Senna obtusifolia</i>	Fabaceae	Annual, biennial, perennial	53	2	55
<i>Tridax procumbens</i>	Asteraceae	Perennial	38	17	55
<i>Achyranthes aspera</i>	Amaranthaceae	Annual, perennial	28	24	52
<i>Datura metel</i>	Solanaceae	Annual, perennial	23	28	51
<i>Dysphania ambrosioides</i>	Amaranthaceae	Annual, perennial	43	8	51
<i>Melia azedarach</i>	Meliaceae	Tree	40	11	51
<i>Acanthospermum hispidum</i>	Asteraceae	Annual	48	1	49
<i>Physalis angulata</i>	Solanaceae	Annual	39	10	49
<i>Amaranthus spinosus</i>	Amaranthaceae	Annual	44	4	48
<i>Phyllanthus amarus</i>	Phyllanthaceae	Annual	15	33	48
<i>Tamarindus indica</i>	Fabaceae	Tree	31	17	48
<i>Anacardium occidentale</i>	Anacardiaceae	Tree	31	16	47
<i>Leucaena leucocephala</i>	Fabaceae	Tree	22	25	47
<i>Mangifera indica</i>	Anacardiaceae	Tree	30	17	47
<i>Psidium guajava</i>	Myrtaceae	Shrub, tree	30	17	47
<i>Mirabilis jalapa</i>	Nyctaginaceae	Perennial	26	20	46
<i>Agave sisalana</i>	Asparagaceae	Perennial, succulent	17	28	45
<i>Carica papaya</i>	Caricaceae	Perennial	15	30	45
<i>Eclipta prostrata</i>	Asteraceae	Annual	42	3	45

Individual regions in which each species occurs can be found in van Kleunen et al. (2019)

(7%), two succulents (5%) and one aquatic species (2%).

The best represented families among these widely distributed naturalized non-natives are Asteraceae (6 species, i.e. 19%), followed by Fabaceae and Amaranthaceae (4 species; 13%). This is different from the distribution of the entire naturalized flora of Africa in families (Table 11.3). Fabaceae, Poaceae and Asteraceae, which are among the richest plant families globally, are also richest in naturalized species in Africa, having more than 600 species in total. Other families are less well represented, having a maximum of 200 species.

The most widely distributed naturalized species in Africa, according to GloNAF, are *L. camara* (reported as invasive from 31 out of 67 regions for which information on invasiveness is available in GloNAF), *Calotropis procera* (26), *A. hispidum* (25), *Tithonia diversifolia* (21), *Pennisetum pedicellatum* (20), *Pontederia crassipes* (formerly *Eichhornia crassipes*) (18), *Fimbristylis lit-*

toralis, *C. odorata* (17), *L. leucocephala*, *Prosopis juliflora* (15), *Digitaria velutina* (14), *Erigeron karvinskianus* (13), *Parthenium hysterophorus* (11), *Imperata cylindrica*, *Pistia stratiotes* and *Salvinia molesta* (10).

11.3.2 Invasive Plants in Natural and Semi-natural Ecosystems

The Distribution of Invasive Plants

We report on the species known to be most widespread, abundant and having the biggest negative impacts within some of the biomes across the continent. The selection of the species in Africa with the greatest impacts on biodiversity and human livelihoods was based on expert opinion, supported by country-level distribution data from the ISC (CABI 2020) and the GISD (ISSG 2015), and data of impacts of invaders gleaned from these and other sources. Those data are often based on insights from other continents/regions; in such cases we assumed that impacts would be

Table 11.3 Families with the greatest numbers of naturalized species in Africa according to data in GloNAF (Pyšek et al. 2017)

Family	Mainland	Island	Mediterranean	Subtropical	Temperate	Tropical	Total
Fabaceae	529	334	110	119	120	514	863
Poaceae	384	298	102	97	132	351	682
Asteraceae	364	249	94	93	126	300	613
Solanaceae	154	91	43	38	34	130	245
Amaranthaceae	145	64	36	52	23	98	209
Brassicaceae	136	63	57	32	35	75	199
Malvaceae	127	69	16	40	21	119	196
Lamiaceae	90	84	21	20	38	95	174
Euphorbiaceae	103	58	22	32	16	91	161
Myrtaceae	91	37	25	7	14	82	128
Rosaceae	75	50	27	14	33	51	125
Convolvulaceae	71	49	16	22	13	69	120
Plantaginaceae	50	54	16	13	30	45	104
Caryophyllaceae	66	30	26	15	16	39	96
Cactaceae	71	23	22	18	7	47	94
Rubiaceae	46	40	3	7	7	69	86
Apocynaceae	53	32	9	10	10	56	85
Polygonaceae	46	39	9	15	18	43	85
Boraginaceae	49	31	19	10	13	38	80
Onagraceae	46	34	12	14	18	36	80

Numbers of species are shown as recorded for mainland vs. island and per zonobiome. Note that the sums across insularity and zonobiomes exceed totals because many species occur in multiple environments

similar across regions/continents, or worse over much of Africa because of people's direct dependence on natural resources. Much of the expert opinion is based on extensive surveys undertaken by one of the authors (ABRW) in eastern and southern Africa, on several studies in South Africa (reviewed in van Wilgen et al. 2020) and on several studies of socio-economic impacts undertaken in the region where impacts are most pronounced [e.g. *C. odorata* (Shackleton et al. 2017c); *L. camara* (Shackleton et al. 2017b); *M. pigra* (Witt et al. 2020a); *M. diplotricha* (Witt et al. 2020b); *O. stricta* (Shackleton et al. 2017d); *T. diversifolia* (Witt et al. 2018); *P. juliflora* (Maundu et al. 2009; Mbaabu et al. 2019)]. Information pertaining to Central, West and North Africa has largely been obtained from the literature and communication with researchers and managers.

Most biomes, vegetation types/formations (White 1983) and regions have been severely invaded by one or more (in many cases numerous) non-native plant species. Arid and semi-arid regions across much of the continent are invaded by *Prosopis* spp. (mesquite). Mesquite invasions are most widespread and have been best studied in eastern Africa (Maundu et al. 2009; Kebede and Coppock 2015; Mbaabu et al. 2019; Shiferawa et al. 2019; Eckert et al. 2020) and South Africa (Shackleton et al. 2015, 2017a). Many Cactaceae species are widespread and impactful invaders (Novoa et al. 2015, 2019); *Opuntia ficus-indica* and *O. stricta* have the greatest invasive ranges (Witt and Luke 2017; Novoa et al. 2019). There are a large number of other invasive Cactaceae species in South Africa's arid lands (Kaplan et al. 2017). *Agave* species, often used as living fences, have escaped cultivation and proliferated in drier areas across Africa, as have *C. procera* (uncertain origin, possibly native in eastern Africa) and *C. gigantea* and species of *Bryophyllum* (native to Madagascar) and *Crassula* species (native in southern Africa). *Parkinsonia aculeata* is also locally abundant in drier areas, especially along dry water courses and floodplains. *Acacia saligna*, abundant and widespread in South Africa, especially in Mediterranean shrublands at the southwestern tip

of the continent (Wilson et al. 2014), is actively used for restoration of degraded ecosystems in other parts of Africa and is emerging as an invader in many regions, as is *A. colei* in some semi-arid parts of the continent.

South Africa's Mediterranean shrublands at the extreme southwestern part of the continent have been severely invaded by numerous non-native trees and shrubs, especially species in the genera *Acacia*, *Hakea*, *Leptospermum* and *Pinus* (Richardson and Cowling 1992; van Wilgen et al. 2016). Although Australian *Acacia* species are actively promoted for agroforestry in other parts of the continent (Richardson et al. 2004), few have become as widespread as invaders as in South Africa, but most species are likely to become major invaders in the future (Richardson et al. 2015). Over much of Africa, it is mainly higher-lying areas that have been heavily invaded to date, especially by *A. melanoxylon* and *A. mearnsii*. *Pinus patula*, *P. pinaster* and *P. radiata* are widespread invaders in South African mountains (Richardson and Brown 1986; Rouget et al. 2002). The Australian acacias mentioned above and several others (notably *A. longifolia*) also invade riparian habitats and other biomes in lower-lying areas (Holmes et al. 2005). The frost-tolerant *Acacia dealbata* is widespread in colder regions of South Africa, while the moderately frost-tolerant *A. decurrens* is abundant in parts of South Africa and Zimbabwe. Several *Rubus* species are abundant and widespread invaders at higher elevations, as is *Biancaea decapetala* which is equally at home at lower elevations. Several *Cotoneaster* and *Pyracantha* species have also proliferated in colder climes, especially in South Africa.

Azadirachta indica and *L. leucocephala* are abundant invaders along the coastline of much of Africa, preferring hot and humid conditions; the latter is still actively planted and is occasionally also locally abundant further inland. Climbers such as *Antigonon leptopus* are often common along coastal zones, while *Ipomoea* species are locally abundant elsewhere together with emerging vines such as *Anredera cordifolia* and *Cardiospermum grandiflorum* where they smother native vegetation. *P. juliflora* thrive in

tropical and subtropical regions, as do other introduced herbs and shrubs, including *Ageratum conyzoides*, *C. odorata*, *Hyptis suaveolens*, *L. camara*, *M. diplotricha*, *P. hysterophorus* and *T. diversifolia*. Most of these species are also abundant in grasslands and savannas over much of Africa. *C. odorata*, which is now common in many countries in central and southern Africa, is abundant in open savanna grasslands, woodlands, riparian zones, forest gaps and edges. *M. diplotricha* has established in similar habitats in many parts of the continent.

Undisturbed African forests have experienced only limited invasions, although gaps created by tree falls, “sustainable utilization” or other types of disturbance are rapidly invaded by many of the species mentioned above. Other species which rapidly invade gaps or forest edges include *Broussonetia papyrifera*, *Clidemia hirta*, *Senna spectabilis*, *Solanum mauritianum* and many species of climbers, notably *A. cordifolia* and *C. grandiflorum*.

Many non-native plants thrive in highly disturbed habitats across a number of biomes. For example, *Argemone* species and *Datura stramonium* are widespread over much of the continent, but are not considered to have significant impacts on biodiversity.

Water bodies are invaded by many non-native plant species which benefit from the presence of water and the regular disturbance associated with these habitats. The semi-aquatic weed *M. pigra* is widespread and abundant around many water bodies, and *Ipomoea carnea* is rapidly expanding its distribution into these habitats. Although *S. molesta* and *P. stratiotes* are widespread, their impacts have been substantially reduced by introduced host-specific biocontrol agents. However, despite the release of multiple biocontrol agents on *Pontederia crassipes* in many countries in Africa, this species is still one of the most widespread invasive aquatic plant species on the continent.

“Transformer” Invasive Plants in Africa

No previous attempt has been made to compile a list of those invasive non-native plants that have the greatest impacts in natural and semi-natural

ecosystems of Africa. Table 11.4 provides a list of species for which there is evidence of invasions that “change the character, condition, form, or nature of ecosystems over substantial areas” (i.e. “transformer species” sensu Richardson et al 2000b). The text below explains the choice of species and discusses the difficulties in collating such information.

South Africa’s first national status report on biological invasions (van Wilgen and Wilson 2017) lists 16 plant species which are considered to have severe impacts on biodiversity and ecosystem services. This list includes seven Australian *Acacia* species: *A. cyclops*, *A. dealbata*, *A. decurrens*, *A. longifolia*, *A. mearnsii*, *A. melanoxylon* and *A. saligna*. Although many of these are present elsewhere in Africa, only *A. mearnsii* and *A. melanoxylon*, and to a lesser extent *A. saligna*, are clearly widespread invaders outside South Africa. Other species with severe impacts in South Africa that are also problematic in other parts of Africa include *C. odorata*, *L. camara* and several *Prosopis* species and their hybrids (of these taxa, *P. juliflora* probably has the greatest impacts). Many of the plant species listed in the South African status report are not known to be present outside of South Africa, or are present but not recorded as causing major damage at this stage. These include many species in the family Cactaceae and many submerged aquatic species. Many *Opuntia* species present in South Africa are under good biological control, and their impacts are regarded as moderate. Many tree species used in forestry and agroforestry, especially *Eucalyptus* and *Pinus* species, have been introduced throughout Africa but are probably under-reported as invaders because of difficulties in distinguishing between species. The status of naturalized and invasive grasses is very poorly known for most of Africa, in contrast to South Africa where knowledge of the status, distribution and impacts of non-native grasses has increased greatly in the last decade (Visser et al. 2016, 2017; Canavan et al. 2021). Only a handful of species of non-native grasses are known to cause major impacts in Africa.

There are also a number of species which are not widespread invaders in South Africa but have

Table 11.4 Twenty widespread and abundant alien plant species considered to have major impacts in terms of transforming natural vegetation over large parts of Africa (“transformer species” sensu Richardson et al. 2000b), with details on habitat types invaded and types of impacts

Species, family, common name and origin	Growth form	Countries where the species has been reported as clearly invasive	Habitat types invaded	Negative impacts
<i>Acacia mearnsii</i> De Wild (Fabaceae); black wattle; temperate Australia	Tree or shrub	Algeria, Botswana Burundi, Eswatini, Ethiopia, Kenya, Madagascar, Malawi, Mozambique, Namibia, Rwanda, Seychelles, South Africa, Tanzania, Uganda, Zimbabwe	Fo, Gr, Tr, Rr, Ha, Pl, Ws, Wc	Displaces natural vegetation, reduces native biodiversity and rangeland productivity. Reduces surface water run-off. Increases soil nitrogen levels, alters soil nutrient cycling
<i>Acacia melanoxylon</i> R. Br (Fabaceae); Australian blackwood; temperate Australia	Tree or shrub	Kenya, South Africa, Tanzania, Zimbabwe	Fo, Gr, Tr, Rr, Ha, Pl, Ws, Wc	Displaces native vegetation, especially in forests and riparian zones, with negative impacts on biodiversity. Increases soil nitrogen levels, altering soil nutrient cycling
<i>Acacia saligna</i> (Labill.) Wendl.; Port Jackson willow; temperate Australia	Tree or shrub	Algeria, Ethiopia, Libya, South Africa		Forms impenetrable thickets which displace native species and prevent their regeneration. Nitrogen fixation creates strong legacy effects that may persist for decades, hindering restoration efforts. Dense stands increase the intensity and frequency of fires and impact negatively on water resources
<i>Azadirachta indica</i> A. Juss. (Meliaceae); neem; northern temperate Asia	Tree or shrub	Ethiopia, Gambia, Ghana, Kenya, Mauritius, Senegal, Tanzania, Uganda	Fo, Sa, Tr, Rr, Ha, Pl, Pa, Ws	Forms dense stands, especially in coastal areas, displacing native plant species. Alters habitats, leading to reductions in the abundance of small mammals
<i>Biancaea decopetala</i> (Roth) O. Deg. (syn. <i>Caesalpinia decapetala</i> (Roth) Alston) (Fabaceae); Mauritius thorn; Tropical Asia	Climber	Burundi, Ethiopia, Kenya, Malawi, Rwanda, South Africa, Tanzania, Uganda	Fo, Sa, TR, Rr, Ha, Pl, Pa, Ws, Wc	Climbs over vegetation, forming tangled, impenetrable thickets which are detrimental to fauna and flora. Grows into forest and woodland canopies, causing canopy collapse. Impedes forest management operations and is a fire hazard. Reduces livestock carrying capacities and inhibits the movement of livestock and people. The large spines cause injuries to wildlife, livestock and people

(continued)

Table 11.4 (continued)

Species, family, common name and origin	Growth form	Countries where the species has been reported as clearly invasive	Habitat types invaded	Negative impacts
<i>Chromolaena odorata</i> (L.) R.M. King & H. Rob. (Asteraceae); <i>Chromolaena</i> ; tropical America	Shrub	Angola, Benin, Cameroon, C. Africa Republic, Congo, DRC, Eswatini, Ghana, Guinea, Kenya, Libya, Mauritania, Mozambique, Nigeria, South Africa, Tanzania, Togo, Uganda, Zimbabwe	Sa, Tr, Rr, Ha, Ar, Pa, Ws, Wc	Displaces native plant species and alters fuel properties of vegetation, leading to increased fire intensities and creating “ladders” that carry fires into the canopies of savanna trees, killing them Reduces the productivity of rangelands and causing serious health problems in livestock and people
<i>Pontederia crassipes</i> Mart. (previously <i>Eichhornia crassipes</i> (Mart.) Solms) (Pontederiaceae); water hyacinth; tropical America	Aquatic	Angola, Benin, Burundi, DRC, Egypt, Ethiopia, Ghana, Kenya, Malawi, Mauritius, Niger, Rwanda, South Africa, Tanzania, Uganda, Zambia, Zimbabwe	Wc, Wt	Forms thick mats which hamper water transport, inhibit or prevent fishing-related activities, block waterways, hamper hydroelectricity generation and provide habitats for vectors of human and animal diseases
<i>Hyptis suaveolens</i> (L.) Poit. (Lamiaceae); pignut; tropical America	Herb	Burkina-Faso, Burundi, Ethiopia, Kenya, Malawi, Tanzania, Uganda, Zambia	Sa, Tr, Rr, Ha, Ar, Pa, Ws	Forms dense stands to the detriment of native fauna and flora. Regarded as one of the worst weeds in the world
<i>Lantana camara</i> L. (Verbenaceae); lantana; tropical America	Tree or shrub	Angola, Burundi, Cape Verde, Congo, DRC, Eswatini, Ethiopia, Gabon, Gambia, Ghana, Guinea, Kenya, Liberia, Madagascar, Malawi, Mauritius, Mayotte, Mozambique, Namibia, Niger, Nigeria, Rwanda, St. Helena, Senegal, Seychelles, South Africa, Sudan, Tanzania, Uganda, Zambia, Zimbabwe	Fo, Sa, Gr, Tr, Rr, Ha, Pl, Ar, Pa, Ws, Wc	Displaces natural vegetation, impacting negatively on biodiversity. Toxic to livestock, causing animal deaths, reduced productivity and loss of pasture
<i>Leucaena leucocephala</i> (Lam.) de Wit (Fabaceae); <i>Leucaena</i> /river tamarind; tropical America	Tree or shrub	Algeria, Botswana, Burundi, Cameroon, Congo, DRC, Ethiopia, Ghana, Kenya, Malawi, Mauritius, Namibia, Rwanda, Seychelles, South Africa, Tanzania, Uganda, Zambia	Sa, Tr, Rr, Ha, Pa, Ws, Wc	Forms large monocultures that displace native plant and animal species. Invasions alter secondary succession processes and render areas unusable and inaccessible
<i>Mimosa diplotricha</i> Sauvalle (Fabaceae); giant sensitive plant; tropical America	Tree or shrub	Burundi, Ethiopia, Ghana, Guinea, Malawi, Niger, Rwanda, Tanzania, Uganda	Fo, Sa, Gr, Tr, Rr, Ha, Pl, Ar, Pa, Ws, Wc	Smothers other plants, shading out light-demanding species and preventing their natural regeneration. Dense stands may prevent or hinder the movement of livestock and wildlife. Plants are toxic to sheep and pigs

(continued)

Table 11.4 (continued)

Species, family, common name and origin	Growth form	Countries where the species has been reported as clearly invasive	Habitat types invaded	Negative impacts
<i>Mimosa pigra</i> L. (Fabaceae); giant sensitive tress; tropical America	Tree or shrub	Burundi, Ethiopia, Ghana, Kenya, Malawi, Mozambique; Namibia, Rwanda, South Africa, Tanzania, Uganda, Zambia	Sa, Tr, Rr, Ha, Ar, Pa, Ws, Wc, Wt	Dense stands can eliminate native plant and animal species and lead to steep declines in the abundance of others. Hampers fishing activities and blocks access to water bodies
<i>Opuntia stricta</i> (Haw.) Haw. (Cactaceae); erect prickly pear; tropical America	Succulent tree or shrub	Angola, Eswatini, Ethiopia, Kenya, Madagascar, Malawi, Mauritius, Namibia, South Africa, Tanzania, Tunisia, Uganda	Sa, Rr, Ha, Pa, Ws, Wc, Dr., Ro	Substantially reduces livestock carrying capacities and access to grazing and water resources. When eaten, causes infections, injury and mortality in livestock
<i>Parthenium hysterophorus</i> L. (Asteraceae); <i>Parthenium</i> ; tropical America	Herb	Botswana, Congo, Djibouti, Egypt, Eswatini, Eritrea, Ethiopia, Kenya, Mauritius, Madagascar, Mauritius, Mayotte, Rwanda, Seychelles, Somalia, South Africa, Tanzania, Uganda, Zimbabwe	Sa, Gr, Tr, Rr, Ha, Ar, Pa, Ws, Wc	Allelopathic and able to suppress natural vegetation. Severely reduces the productivity of rangelands and causes serious allergenic reactions (dermatitis, hay fever and asthma) in a large proportion of people who come into contact with it, as well as in livestock and wildlife
<i>Pinus patula</i> Schiede ex Schltdl. & Cham. (Pinaceae); patula pine Mexico	Tree or shrub	Botswana, Kenya, Madagascar, Malawi, South Africa, Tanzania, Zimbabwe	Fo, Gr, TR, Rr, Ha, Pl, Pa, Ws, Wc	Forms dense stands, displacing native plant and animal species and reducing water run-off. Considered to be one of the most aggressive invaders of Afromontane forests and grasslands
<i>Prosopis juliflora</i> (Fabaceae); mesquite; tropical America	Tree or shrub	Chad, Djibouti, Egypt, Eritrea, Ethiopia, Kenya, Malawi, Mauritania, Mozambique, Namibia, Niger, Nigeria, Senegal, Somalia, Sudan, Tanzania, Uganda	Sa, Tr, Rr, Ha, Ar, Pa, Ws, Wc	Reduces grazing capacity, eliminates many species from invaded ecosystems and depletes groundwater resources. Despite some benefits in the form of firewood and edible pods, the overall net economic contribution is negative and set to worsen as the species continues to spread
<i>Psidium guajava</i> L. (Myrtaceae); guava; tropical America	Tree or shrub	Burundi, Congo, Eswatini, Ethiopia, Kenya, Malawi, Mayotte, Rwanda, South Africa, Tanzania, Uganda, Zambia	Fo, Sa, Tr, Rr, Ha, Pl, Pa, Ws, Wc	Establishes dense stands, displacing native plant and animal species. Allelopathic, impacting negatively on some crop species

(continued)

Table 11.4 (continued)

Species, family, common name and origin	Growth form	Countries where the species has been reported as clearly invasive	Habitat types invaded	Negative impacts
<i>Solanum mauritianum</i> Scop. (Solanaceae); bugweed; South America	Tree or shrub	Cameroon, Congo, Eswatini, Kenya, Madagascar, Mauritius, Rwanda, South Africa, Tanzania, Uganda	Fo, Tr, Rr, Ha, Pl, Ws, Wc	Displaces native plants and animals. Copious production of fleshy fruits disrupts vertebrate-mediated seed dispersal of native plant species, leading to declines in native species richness. The plant is toxic to livestock
<i>Tithonia diversifolia</i> (Hemsl.) A. Gray (Asteraceae); Mexican sunflower; tropical America	Shrub	Burundi, Cameroon, DRC, Egypt, Eritrea, Ethiopia, Kenya, Malawi, Mozambique, Niger, Rwanda, South Africa, Tanzania, Uganda, Zambia, Zimbabwe	Sa, Tr, Rr, Ha, Pl, Ar, Pa, Ws, Wc	Displaces native vegetation and reduces species diversity and the productivity of rangelands. Contributes to local extinction of valued native species
<i>Tithonia rotundifolia</i> (Mill.) S.F. Blake (Asteraceae); red sunflower; North America	Tree or shrub	Botswana, Kenya, Malawi, South Africa, Tanzania, Uganda, Zambia, Zimbabwe	Sa, Tr, Rr, Ha, Ar, Ws	Forms dense stands to the detriment of native fauna and flora and alters ecosystem services

Data on countries invaded are mainly from CABI (2020), ISSG (2015), Witt and Luke (2017) and A.B.R. Witt (unpubl data)

Fo forest, Sa savanna, Gr grassland, Tr transformed, Rr road/railside, Ha around habitation, Pl plantation, Ar arable/ploughed land, Pa pastoral, Ws wasteland, Wc watercourse, Wt wetland, Dr dryland/well drained, Kl kloof/ravine, Ro rocky site

major impacts in other parts of the continent. These species include *Acacia colei*, *Agave angustifolia*, *A. indica*, *Calliandra houstoniana*, *C. hirta*, *Dahlia imperialis*, *H. suaveolens*, *M. diplotricha* and *S. spectabilis*. Although the distribution of some of these species is still localized, impacts are severe but poorly studied. *Azadirachta indica* and *H. suaveolens* were selected for inclusion in Table 11.4 because of their widespread distribution and well-documented impacts.

South Africa has many more widespread and highly problematic invasive plant species than any other African country. However, the species that are present elsewhere in Africa are widespread and probably have greater impacts on human livelihoods than in South Africa (De Groote et al. 2003; Maundu et al. 2009; Mwangi and Swallow 2008; Shackleton et al. 2017a, b, c; Witt et al. 2018, 2019). This is mainly because a large proportion of people in Africa outside South Africa depend directly on natural resources for their survival. Species across the whole continent which we consider to have the biggest negative impacts

on biodiversity and livelihoods include *Acacia mearnsii*, *C. odorata*, *L. camara*, *P. hysterophorus*, *P. crassipes*, *P. juliflora*, and *T. diversifolia*. Other highly problematic species are *A. indica*, *Biancaea decapetala* (previously *Caesalpinia decapetala*), *H. suaveolens*, *L. leucocephala*, *M. pigra*, *M. diplotricha*, *Tithonia rotundifolia* and to a lesser extent *Pinus patula*, *Psidium guajava* and *S. mauritianum*. A number of *Senna* species are fairly widespread, but their impacts are less severe, although *S. spectabilis* forms dense stands in disturbed forests. *Datura stramonium* and *Xanthium strumarium* are widespread but invade mainly highly disturbed areas, so their impacts are limited. *Ricinus communis*, considered by some to be introduced to tropical Africa (Foster et al. 2010), is another widespread species, but there are few reports of impacts of this species. Of the many invasive Cactaceae species, *O. stricta* is the most serious transformer; it has established significant localized populations in Kenya, Malawi and Namibia and has major negative impacts in Kenya (Shackleton et al. 2017d).

A number of invasive species which are widespread and abundant in South Africa are emerging weeds across much of the rest of the continent. These include the climbers *A. cordifolia*, *C. grandiflorum*, *Cuscuta campestris*, *Dolichandra unguis-cati*, *Thunbergia grandiflora*, several *Passiflora* and *Ipomoea* species and possibly also *Pereskia aculeata*. *Cryptostegia grandiflora* is already abundant locally in Ethiopia and in parts of southern Africa and has huge potential for further spread in Africa (Kriticos et al. 2003). *Antigonon leptopus* is another climber which is locally abundant in many parts of Africa and which is likely to expand its range.

Herbs are often under-reported during surveys of non-native plants. *Senecio madagascariensis*, native to southern Africa and Madagascar, is already present in eastern Africa and likely to become increasingly problematic, as is another daisy, *Verbesina encelioides*. Species of trees and shrubs that are already well established in many parts of Africa (e.g. *A. colei*, *A. melanoxylon*, *Broussonetia papyrifera*, *C. houstoniana*, *Calotropis gigantea*, *D. imperialis*, *I. carnea*, *Montanoa hibiscifolia* and *Tecoma stans*) are likely to expand their ranges. Some cacti species, such as *Opuntia elatior* and *O. engelmannii*, for which no biological control agents have been released yet, are locally abundant and likely to expand, while *Cereus jamaru* is naturalized in eastern Africa. Waterweeds such as *P. stratiotes* and *S. molesta* are under relatively good biological control throughout much of the continent. However, we expect emergent species such as *Limnobium laevigatum*, and possibly *Limnocharis flava*, to expand their distributions.

11.3.3 Impacts of Invasive Plants in Africa

Worldwide, “weeds” cause losses in crop yield of about 10% in low-middle-income countries and of about 25% in low-income countries, many of which are in Africa (Akobundu 1987). For example, yields of sorghum in experimental fields in Ethiopia, with dense *Parthenium hysterophorus* invasions, were reduced by 97% (Tamado et al.

2002). In the Ethiopian lowlands, *Parthenium* is now considered by 90% of farmers to be the most damaging weed in both croplands and grazing areas (Tamado and Milberg 2000). Farah and Al-Abdulsalam (2004) recorded yield losses of more than 50% in hyacinth bean, lentil, chickpea, faba bean, lucerne and fodder pea as a result of invasions by *Cuscuta campestris* in Egypt. *Lantana camara* invasions were reported to reduce yields of maize and cassava by 26–50% by 40% of respondent households in Uganda (Shackleton et al. 2017a), while 90% of respondents in northern Tanzania reported that *Chromolaena odorata* reduced crop yields (Shackleton et al. 2017b).

Invasive plant species also have dramatic impacts on livestock production in many parts of Africa. Van Wilgen et al. (2008) suggested that natural grazing capacity in South Africa would be reduced by 71% without management of invasive plants. Invasions of *C. odorata* in South Africa have reduced the carrying capacities of pastures from about six hectares per livestock unit (LSU) to more than 15 ha/LSU (Goodall and Morley 1995). In Ethiopia, invasive *Prosopis juliflora* has reduced understorey basal cover for perennial grasses from 68% to 2% and has reduced the number of grass species from seven to two (Kebede and Coppock 2015). Invasions of *Opuntia stricta* in Laikipia, Kenya, not only reduce the availability of forage but are also have dramatic impacts on livestock health (Shackleton et al. 2017c).

Plant invasions have dramatic impacts on water resources. Such impacts have been thoroughly assessed only for South Africa where reductions in surface water run-off of 3300 million m³ (about 7% of the national total) have been attributed to invasive plants (Le Maitre et al. 2000). Declines in water run-off in South Africa, attributed to invasions of *Acacia mearnsii* alone, amount to an estimated 577 million m³ annually (Versfeld et al. 1998). Introduced pines (*Pinus* spp.) have escaped from cultivation in many parts of South Africa (van Wilgen and Richardson 2012) and have had a dramatic impact on water resources. In the Drakensberg in Kwazulu-Natal, pine plantations have reduced streamflows by

82% (Bosch 1979), while in the Western Cape, streamflow from invaded fynbos catchments have declined by 55%. If the terrestrial invasive plants currently present in South Africa were left to expand their distribution and to occupy their full potential ranges (Rouget et al. 2004), water losses would increase to about 56% of the national total (van Wilgen et al. 2008).

Invasions of water hyacinth (*Pontederia crassipes*) and of other waterweeds can also dramatically increase water losses, impacting on many sectors. In southern Benin, water hyacinth invasions reduced the annual income of 200,000 people by about US\$ 84 million (de Groot et al. 2003). More than two decades ago, invasive water hyacinth was estimated to cost seven African countries US\$ 20–50 million per year in impact and management costs (Joffe and Cooke 1997). Water hyacinth is now invasive in almost 20 countries across the continent and causes major impacts on water transport, thwarts or even prevents fishing-related activities, blocks waterways and canals and hampers hydroelectricity generation while also providing breeding sites for vectors of human and animal diseases (Burton 1960; Gopal and Sharma 1981; Viswam et al. 1989).

Invasive plants have major negative impacts on human and animal health. For example, *P. hysterophorus* causes severe allergenic reactions in people who regularly come into contact with the plant (Patel 2011). In Ethiopia, symptoms recorded in people who have come into contact with the weed on a regular basis include general illness, asthma, irritation of skin and pustules on the hands, stretching and cracking of the skin and stomach pains (Wiesner 2008). Paper mulberry (*Broussonetia papyrifera*), a tree that is invasive in at least Ghana, Malawi and Uganda, produces large quantities of allergenic pollen which exacerbates asthma in sufferers. We know of no attempt to quantify its impacts in Africa, but in Islamabad, Pakistan, *B. papyrifera* sometimes accounts for as much as 75% of the total pollen

count, contributing to ill health or even death in elderly and infirm people.

Biodiversity is also negatively affected by invasive plants in many ways. In South Africa, dense stands of invasive plants reduce the richness of native species, e.g. in the fynbos (Richardson et al. 1989) and Nama Karoo, Succulent Karoo and savanna biomes (Shackleton et al. 2015). Thickets of invasive *C. odorata* have negative impacts on the breeding biology of the Nile crocodile (Leslie and Spotila 2001), while in Cameroon this invader displaces native species in the family Zingiberaceae which are an important food source for endangered western lowland gorillas (van der Hoeven and Prins 2007). In Lochinvar National Park, Zambia, invasions of *Mimosa pigra* have reduced bird diversity by almost 50% and bird abundance by more than 95% (Shanungu 2009). In South Africa, *Prosopis* invasions have reduced bird species diversity in some guilds by more than 50% (Dean et al. 2002). Plant invasions in many parts of Africa have caused a dramatic change in vegetation structure, although the implications of such changes for ecosystem functioning have only been studied in a few cases, mostly in South Africa. For example, invasions of non-native trees and shrubs have important effects on the fire regime in fynbos (van Wilgen and Richardson 1985) and transform riparian vegetation with profound implications for the stability of riverbanks and the functioning of river ecosystems in many parts of South Africa (Holmes et al. 2008). Nitrogen-fixing invaders, notably Australian *Acacia* species, cause many diverse impacts in invaded ecosystems that may persist for decades after invasive stands are cleared (Le Maitre et al. 2011).

Many introduced plants that become invasive, unlike invasive species in some other taxonomic groups such as insect crop pests, have cross-cutting impacts that affect multiple sectors, ranging from biodiversity to agriculture and pastoralism and from water resources to human and animal health. Once invasive plants are wide-

spread and abundant, eradication becomes impossible, and their impacts on natural and human-modified ecosystems become permanent, requiring increasingly expensive management which is often thwarted by financial constraints. Invasive non-native plants pose a rapidly escalating threat to livelihoods and economic progress in Africa, where many people depend directly on natural resources for their survival.

11.3.4 Management of Invasive Plants in Africa

Most African countries are signatories to the Convention on Biological Diversity (CBD) and are obligated to manage invasive non-native species. Many of the Sustainable Development Goals (SDGs) also refer to invasive species or can only be achieved if invaders are effectively managed (Egoh et al. 2020). However, effective management of biological invasions in most parts of Africa is hindered by a number of issues. The main barriers to invasive plant management in Africa, with the possible exception of South Africa where there are a number of national initiatives to manage invasions (van Wilgen et al. 2020), are weak policies and institutional environments; a lack of awareness and the dearth of critical information; a general lack of capacity; and inadequate arrangements and coordination for prevention and control (Boy and Witt 2013). Low levels of human capacity and associated resources translate into a shortage or total lack of data on the presence, distribution and impacts of invasive species. This thwarts attempts to create awareness, especially among policymakers who require robust data, especially on impacts, to develop policies and to justify the allocation of resources for effective management. Many development agencies have initiated projects to generate information on the presence and impacts of invasive plants in a number of countries and regions throughout Africa. These initiatives are beginning to bear fruit, with an increase in the number of students and scientists undertaking studies on the impacts of invasive plants in Africa, although national funding to support such activi-

ties is limited. Most research, and even management interventions, is still funded by international donors. Despite the increasing availability of information on the negative impacts of invasive plants on biodiversity and livelihoods, management of biological invasions is still poorly funded, if at all, by most African governments.

Outside South Africa, most management interventions have been undertaken in protected areas. For example, *Senna spectabilis* was targeted in Budongo Forest Reserve in Uganda; *P. juliflora* in Awash National Park (NP) in Ethiopia; *B. papyrifera* in Afram Headwaters Forest Reserve in Ghana; and *L. camara* and *Mimosa pigra* L. in Mosi-oa-Tunya and Lochinvar NPs in Zambia, respectively. Other donor-funded projects include the manual control of the native weedy species *Solanum campylacanthum* in Nakuru and Amboseli NPs and *O. stricta* in Tsavo East NP, Kenya. Some funds were also made available to manage *L. camara* in Ol Donyo Sabuk NP, Kenya, and Queen Elizabeth NP in Uganda. There has also been a project to manage *Senna spectabilis* in Mahale Mountains NP, Tanzania (Wakibara and Mnaya 2002), and a number of other ad hoc management interventions in other protected areas.

Several initiatives have been launched to control *Prosopis* species at a broader level. For example, in 1995 the Government of Sudan issued a Presidential Decree that invasive mesquite should be eradicated. This resulted in a plethora of management interventions, none of which were successful, mainly due to a lack of sustainable long-term funding (Suliman et al. 2015). In eastern Africa, management efforts have largely focussed on “control through utilization” (Choge et al. 2007). The reasoning behind this intervention is that intensive utilization of tree products such as the pods for animal and human consumption and the biomass for fuelwood and charcoal would be a cost-effective control option. However, the continued spread and densification of mesquite show that this strategy has had no or little impact. Indeed, it has probably exacerbated the problem by encouraging people to establish plants throughout the region. Placing any value on an invasive species is prob-

lematical as it creates incentives for retaining rather than removing the species. National strategies for dealing with *Prosopis* invasions have been implemented or are proposed for several countries (Shackleton et al. 2017d; MOLF 2017; S. Choge pers. comm.). In 2015, an international and multidisciplinary project was launched on “Woody invasive alien species in eastern Africa” (<http://woodyweeds.org>). Focussing on Ethiopia, Kenya and Tanzania, the project aims to assess and mitigate the impacts of woody invasive plants on ecosystems and rural livelihoods. *Prosopis* spp., *L. camara* and *C. odorata* are listed as the focus of the project, but most work has been done on *P. juliflora*. This is a promising project and could serve as a model for regional cooperation to deal with other major plant invaders in other parts of the continent.

Several countries have attempted to control *P. crassipes* by utilizing the biomass for various purposes. Most of these interventions have been unsuccessful in reducing the density or distribution of the target species which continues to densify and spread.

The efficacy of many interventions against invasive plant in Africa has been inhibited by the lack of registered herbicides in most countries. The cost of registering herbicides is largely prohibitive and is only funded by manufacturers if the potential market warrants the investment. Without national programmes to manage invasive plants and actions that compel landowners to control invasive plants, the market will remain small.

Once established, biological control agents can provide effective and sustainable control of the target species across much of its range within a country or a region, or in some cases across the continent without the need for additional financial inputs. More than 200 invasive plant species have been targeted for biological control worldwide, resulting in the intentional release of over 500 biological control agents with over 90 countries having intentionally released at least one biological control agent (Winston et al. 2014). In Africa, not including South Africa, 29 countries have intentionally released 38 biological control agents against 17 invasive plant species, resulting

in the successful control of 12 species (71%), according to local expert opinion (Day and Witt 2019). South Africa has released 103 agents against 51 invasive plant species, followed by Zambia which has intentionally released 16 biological control agents against 4 species, resulting in the control of 2 species (Winston et al. 2014). Most biological control efforts in Africa outside of South Africa have been against the three main water weeds (*P. crassipes*, *Pistia stratiotes* and *Salvinia molesta*); control or partial control has been achieved in most countries where the agents have established (Mbatia and Neuenschwander 2005; Coetzee et al. 2009; Julien et al. 2009; Neuenschwander et al. 2009; Winston et al. 2014). In resource-poor countries, biological control remains the most cost-effective management option. Despite this it has not been embraced across the continent or supported by many donors. This is probably because of a lack of knowledge and awareness on the current and potential future impacts of invasive plants and the safety and efficacy of weed biological control. A lack of the required infrastructure and capacity, conflicts of interest and insufficient funding are other barriers (Day et al. 2020). These barriers are being overcome as more information on the impacts of invasive plants is being generated across the continent. Capacity in the field is also growing. There is now a need for governments to implement strategies and action plans and to fund national programmes. There is also an imperative for increased cooperation and collaboration between all stakeholders, especially government departments, to tackle plants systematically. Since invasive plants cannot be managed in isolation, increased cooperation between countries within regions is also required in order to share information, especially on feasible management interventions, and most importantly to pool resources to manage shared problems.

11.4 Discussion

Analysis of the GloNAF database has provided a useful list of naturalized plant species in Africa. However, many widespread non-native species

that invade and have major impacts in natural areas are missing from this database. There is clearly an urgent need for much better information on the status of non-native plants for the whole continent. Systematic surveys of transformer invaders of natural areas have not been done for most of the continent. Our current knowledge (as summarized in this chapter) is based on detailed information from a few countries, notably South Africa, and extrapolations, aided by rapid surveys in some other regions across the continent. Systematic surveys need to be done for many more countries, ideally using standardized methods and definitions, to provide an accurate picture of the status of non-native plants for the continent. Besides GloNAF, the following resources are crucial to support developments and advances in this regard:

- CABI produces the **Invasive Species Compendium (ISC)** (www.cabi.org/isc) which aims to be a one-stop shop for information on invasive species and their effects on natural and managed ecosystems. The ISC focusses on species with the greatest impacts. Launched in 2012, ISC is funded by an international consortium comprising a wide range of organizations, including government departments, NGOs and private companies. It has detailed data sheets for more than 2600 species, some 900 of which are plant species that are either invasive in Africa or native to Africa and invasive elsewhere. More basic data sheets are available for another 8000 invasive species.
- The **Global Invasive Species Database (GISD)** is a free, online searchable source of information about non-native and invasive species that negatively impact biodiversity. It focusses on invasive non-native species that threaten native biodiversity and natural areas and covers all taxonomic groups from microorganisms to animals and plants. Managed by the Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission, it was developed between 1998 and 2000 as part of the global initiative on invasive species led by the Global Invasive Species Programme (GISP). The

ISSG is currently working with partners on a global initiative developing the Global Register of Introduced and Invasive Species (GRIIS) which is aimed at developing validated, verified and annotated inventories of introduced and invasive species.

- The **Global Biodiversity Information Facility (GBIF)** is an international network and research infrastructure funded by governments and aimed at providing open access to data about all types of life on Earth. Much of the data, submitted by approved/verified experts, is on the distribution of invasive plants. However, it is currently difficult to disentangle, check and verify non-native plant distribution data from GBIF. Planned improvements in this context will greatly improve the usefulness of GBIF data for research and management of plant invasions in Africa.
- There is huge potential for citizen science platforms such as **iNaturalist** to feed information into inventories at the scale of countries, regions and protected areas.

Protocols must be implemented to draw on the abovementioned resources to feed into national and regional initiatives, several of which have already made important contributions. The Field Guide to the Naturalized and Invasive Plants of Eastern Africa (Witt and Luke 2017) provides a comprehensive review of problematic plants in Ethiopia, Kenya, Uganda, Tanzania and Rwanda. Current initiatives include the development of a Field Guide to the Naturalized and Invasive Plants of Malawi and Zambia (due for completion in 2021).

In many parts of Africa, widespread plantings of non-native plant species are fairly recent. Given the time lags between introduction/planting and the emergence of widespread invasions that are well documented worldwide, there is no doubt that large parts of the continent have a large invasion debt (*sensu* Rouget et al. 2016). Species that are invasive in one part of the continent are very likely to invade in other areas. Lessons must be learned from regions with longer histories of widespread use of non-native plants in agroforestry, commercial forestry, ornamental horticultural

ture and other sectors known to be important pathways of introduction and dissemination of invasive plants (see discussion in Richardson et al. 2015). Large-scale tree planting projects are underway or are planned for many parts of Africa, and in many cases non-native species known to be invasive are being planted, or are earmarked for planting (Brundu et al. 2020). Assessments of the risk of invasions and resulting negative impacts must be an integral part of the planning of such projects.

Only South Africa has a long history of effective, sustained and systematic management of invasive plants (reviewed in van Wilgen et al. 2020). Several other countries have launched promising initiatives, and national strategic plans have been published or are in preparation in several countries. Effective management of invasive plants in Africa clearly requires a radical improvement in collaboration between countries. We propose some key changes that are needed to improve the effectiveness of management of plant invasions at the regional level in Africa.

- Many countries share the same invasive plant species, and there is a need to share experiences on successes, failures and opportunities for management. Shared insights could improve methods for dealing with key species or categories of species (e.g. Wilson et al. 2011; Brundu et al. 2020), create standardized approaches for dealing with conflict-generating non-native plants (Kull et al. 2011; van Wilgen and Richardson 2014; Hirsch et al. 2020) and provide guidelines for developing national strategies for key species (e.g. van Wilgen et al. 2011; Shackleton et al. 2017a) and protocols for effective engagement with stakeholders (e.g. Novoa et al. 2018).
- Standardized approaches should be developed or customized for assessing impacts on biodiversity and human livelihoods in Africa (the EICAT and SEICAT schemes are recommended; Blackburn et al. 2014; Bacher et al. 2018).
- Transparent protocols are needed for prioritizing invasive species to target for manage-

ment. These will rely on accurate and up-to-date data on distribution and impacts. Priority should be given to species and sites where impacts are currently greatest or where interventions can prevent the realization of major impacts in the future. Priority should be given to species with the potential to cause irreversible impacts or “regime shifts” (Gaertner et al. 2014; Shackleton et al. 2018).

- Objective frameworks for monitoring, including indicators, are essential for assessing trajectories of invasions and the effectiveness of interventions. The 2017 report on “The status of biological invasions and their management in South Africa” (van Wilgen and Wilson 2017) and the indicators for monitoring biological invasions at a national level developed for South Africa (Wilson et al. 2018) could serve as models for other countries.
- Effective research networks need to be expanded to serve the whole continent. Only one country (South Africa) has a research centre dedicated to research, capacity development, service provision, information brokerage and networking in the field of biological invasions (Richardson et al. 2020a). There is scope to replicate this model in other parts of the continent, as has been proposed for BRICS countries (Measey et al. 2019).

11.5 Conclusions

Knowledge on the presence, distribution and impacts of invasive non-native plants is uneven for African countries. Drawing on a global database of naturalized plants, diverse published and unpublished sources and correspondence with regional authorities, this chapter provides an assessment of the state of knowledge. Many invasive plant species have major negative impacts on biodiversity, on ecosystem services and on human livelihoods, and impacts are increasing rapidly. Some successes have been achieved with managing species in a few regions, but most physical and chemical control interventions have been ad

hoc, short-lived and reliant on donor funds. Biological control offers sustainable solutions for many species and should be endorsed more widely. Standardized approaches for quantifying distribution and impacts and coordination between various stakeholders in-country, across regions and at the continental level are urgently needed to improve the effectiveness of management.

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Island Plant Invasions

12

Kelsey C. Brock and Curtis C. Daehler

Abstract

Despite accounting for less than 5% of Earth's total land area, over one-quarter of the world's plant diversity is native to islands, and many of these species are endemics. Islands have long been recognized as hotspots for plant invasions, hosting proportionally more naturalized species than similarly sized continental areas. Recent estimates suggest that more than a quarter of island floras now have more non-natives than natives. Thus, remote island floras represent a unique conservation problem where high numbers of endemic species, which can be thought of as globally rare, co-occur and interact with disproportionately high numbers of non-natives, which are often widespread species at the global scale. Known and presumed negative interactions between invasive and native plant species have motivated many conservation efforts, prompting numerous studies as well as speculation about the future of island biodiversity. For this review, we focus on plant invasions on oceanic islands, where human-related transport is the main source of non-native species arrivals. The small spatial scale of many oceanic islands can facilitate rapid population and

community responses to invasion, but small spatial scales also increase the feasibility of effective management, and a continuous oceanic border can present a special opportunity to implement effective biosecurity aimed at preventing invasions.

Keywords

Islands · Invasive plants · Dispersal · Naturalization · Impacts · Biosecurity · Management

12.1 Introduction

Islands are characterized by distinct boundaries, and their biodiversity dynamics have been generalized within the framework of island biogeography theory. MacArthur and Wilson's (1967) equilibrium theory of island biogeography provided the first model to understand species richness as a function of island area and remoteness, inspiring the use of islands as model systems to uncover foundational patterns in ecology and evolution. Our modern understanding of biogeography is largely owed to island studies, extending beyond the traditional concept of land surrounded by water to include patches of suitable habitat surrounded by human disturbance for use in conservation planning. This review focuses on terrestrial islands surrounded by oce-

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anic waters and includes both continental islands, which are defined as being at one time connected to a continent, and volcanic islands that arose devoid of life. Volcanic islands, which vary in their remoteness and often host unique life forms, present diverse biotic and abiotic contexts that can provide unique insights into invasion processes and impacts. Despite extraordinary developments in island biogeography in the last 50 years, ample opportunity exists to further use islands to understand the dynamics between native and non-native species as humans continue to disperse species across the globe at unprecedented rates. To guide conservation planning, studies are urgently needed to predict how invasions affect biodiversity on islands in combination with climate change and habitat alteration. Moreover, island systems may provide a lens to help view the future of continental systems (Vitousek 2002), emphasizing the broader insights that may be gained from understanding invasion patterns on islands.

12.2 Patterns on Islands

12.2.1 Plant Species Arrival and Diversification

Remoteness and Modes of Dispersal

After accounting for differences in area, endemic richness is approximately 9.5 times higher on islands than in mainland regions, and thus, native island floras are typified by uniqueness (Kier et al. 2009). However, islands often have lower total native species richness in comparison with continents, especially for islands less than 10,000 km² (Whittaker and Fernández-Palacios 2007; Kreft et al. 2008; Weigelt et al. 2013; Whittaker et al. 2017). A major reason these unique, albeit comparatively depauperate, native floras arise on islands is because only certain plant lineages are naturally capable of long-distance dispersal across oceans (Carlquist 1967; Weigelt et al. 2015). Diminishing dispersal success across long distances is reflected by a pattern of decreasing native species richness with increasing island isolation (MacArthur and

Wilson 1967). The effect of dispersal limitation on island plant richness is perhaps best demonstrated by the comparatively higher native species richness per unit area found on continental versus volcanic islands (Kreft et al. 2008). Continental islands host more mainland lineages that were able to disperse across land or short distances over water (Weigelt et al. 2015). This results in continental islands being an exception to the species-isolation relationship observed for other islands, such that remoteness of continental islands is not always clearly related to species richness (Kreft et al. 2008; Weigelt and Kreft 2013). In contrast, islands arising from the mid-ocean volcanic activity must be newly colonized via long-distance dispersal.

The oceanic barriers that once played a dominant role in community assembly on islands have now been superseded by purposeful or accidental transport by humans (Fig. 12.1; Sax and Gaines 2008; van Kleunen et al. 2015b; Dawson et al. 2017; Pyšek et al. 2017). Therefore, wholly different plant characteristics may increase the odds of contemporary long-distance transport. Whereas native plant lineages on islands are overrepresented by bird, ocean, or wind-dispersed colonists (Carlquist 1967; Cain et al. 2000; Gillespie et al. 2012, but see Vargas et al. 2012), humans most frequently import plants to islands for ornamental or agricultural purposes (Hulme et al. 2008); thus, rather than selecting for dispersal traits, these plants were selected for traits that promote ease of cultivation (e.g., high germination, growth rate, hardiness) and attractiveness to people (e.g., showiness of flowers, plant size), and these traits tend to be present in a large proportion of naturalized species (van Kleunen et al. 2015a). However, various additional human-related introduction pathways may promote different plant traits, including small seeds that are accidentally transported as contaminants in seed mixes or in soil adhering to vehicles and equipment, which may be transported to islands by ship or airplane (Hulme et al. 2008). Overall, human introductions incorporate a greater diversity of plant traits as well as phylogenetic diversity relative to those present in native island

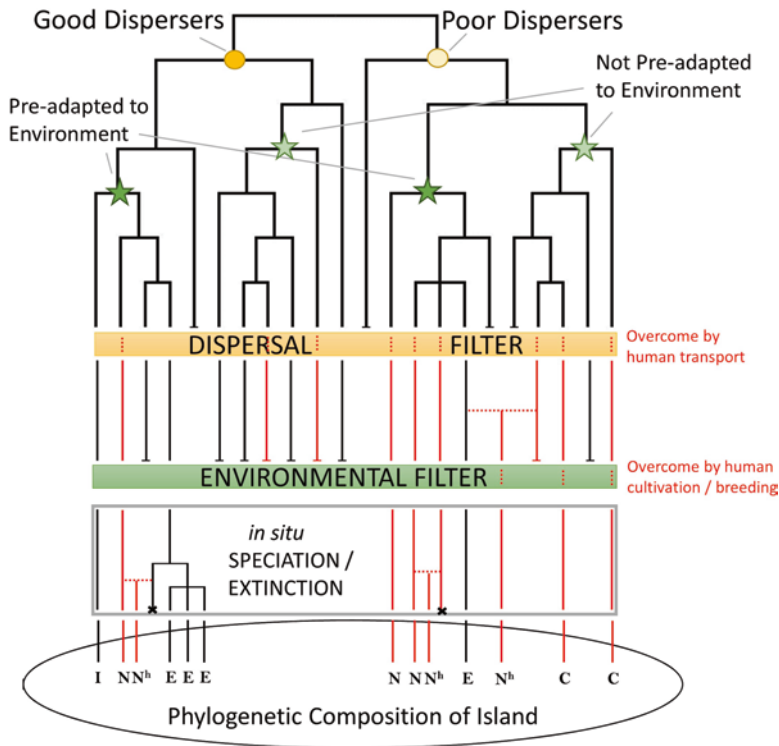


Fig. 12.1 Dispersal, environment, in situ speciation/extinction, hybridization, and human assistance as determinants of native (black lines) and non-native (red lines) plant phylogenetic composition on islands, where *I* = Indigenous, *E* = Endemic, *N* = Naturalized, *Nh* = Naturalized hybrid, *C* = Cultivated, and *x* denotes in situ extinction/extirpation; expanded from Weigelt et al.'s (2015) framework for native island species. Dotted lines

between lineages represent hybridization events, including between non-natives and between non-native and endemic species. Dotted lines through filters represent instances where human activity allows lineages to overcome barriers to colonize islands, including the transport of poor dispersers and the cultivation (*C*) or interbreeding (rightmost *Nh*) to facilitate acclimation

floras, resulting in major structural changes to island floras.

Environmental and Habitat Filtering

Regardless of whether a colonist arrives by natural or human means, species are subject to similar environment or habitat filtering, where an island's species composition is determined by the presence of suitable environmental conditions and habitat availability (Fig. 12.1; Weigelt et al. 2015). Both native and non-native plant species richness on islands have been correlated with island size and elevation, which are generally associated with habitat diversity (Kohn and Walsh 1994; Ricklefs and Lovette 1999; Blackburn et al. 2016). High-elevation islands

display rain shadow effects, leading to strong gradients in precipitation on these islands, while temperature decreases with elevation, creating a surprisingly wide variety of climatic conditions for colonists (Leuschner 1996). For example, the Hawaiian archipelago has distinct wet and dry zones that differ in precipitation by over 20× between windward and leeward sides, and although tropical in latitude, freezing alpine zones occur at high elevations (Peel et al. 2007; Giambelluca et al. 2013). Colonization by plant species from temperate continental areas is documented in Hawai'i for both native and non-native species. Approximately 28% of the native flora is thought to be derived from temperate lineages (Price and Wagner 2018), and although the pro-

portion of naturalized species from temperate lineages is not known, the ratio of temperate to tropical species increases with elevation, and hundreds of temperate species have naturalized in upper-montane habitats (Daehler 2005).

While high-elevation islands such as Hawai'i exemplify habitat diversity, atolls are simplified landmasses with little elevation change and no orographic rainfall, representing the final stage of a volcanic island's life before submergence (Whittaker et al. 2017). Therefore, habitat diversity is low, and plants on these flat landscapes experience saline, soils with high levels of calcium carbonate and windy conditions and may be subject to inundation during extreme weather events (Kreft et al. 2008; Mueller-Dombois and Fosberg 2013). A recent study of 111 atolls described a range of 3–176 native plant species per island, with richness increasing with even small gains in maximum island elevation (Larrue et al. 2018). Despite comparatively low habitat diversity, Larrue et al. (2018) found that 22% of the sampled atolls harbored endemic species and that endemism was correlated with both elevation and distance to other raised atolls, signifying the importance of both habitat diversity and cross-oceanic dispersal in determining species richness. Non-native plant diversity has so far been little studied on atolls, although non-native species richness has been positively associated with maximum island elevation in general (Denslow et al. 2009); it is reasonable to suspect that homogenous atoll landscapes are able to host fewer naturalized plants than higher islands.

In Situ Speciation and Phylogenetic Diversity

Although dispersal ability and environmental filtering results in biota being biased toward certain taxonomic groups, a significant driver of floristic uniqueness on islands is the radiation of founding lineages to generate endemic species. This phenomenon is especially apparent on remote islands; the number of endemic island taxa increases with distance from mainland or neighboring island (Gillespie et al. 2008). On very remote islands, low natural immigration rates, especially when accompanied by a diversity of

available habitats, mean that speciation through adaptive radiation can become the main driver of species diversity. Adaptive radiations, which are defined as the rise of species diversity via the adaptation of a lineage to different environments, are thought to be more probable when a colonizing lineage is presented with a diversity of habitats unoccupied by other competitors (Givnish 2010; Ponisio et al. 2019)—a condition that readily arises on remote, volcanic islands where elevation and erosion patterns provide both habitat diversity and opportunities for isolation among habitats (Whittaker et al. 2008). Although species richness on these islands can be quite high due to adaptive radiations, phylogenetic diversity, a measure of biodiversity that accounts for evolutionary origin, is low because the total island diversity arises from few colonists (Fig. 12.1; Forest et al. 2007; Weigelt et al. 2015). For instance, all 1039 native vascular plant species in Hawai'i are thought to have arisen from just 259 original founders, generating a native flora that is now 90% endemic (Price and Wagner 2018). Consideration of phylogenetic relationships is important because research on islands continues to be inspired by the hypotheses that invaders that are closely related to natives will be less successful (Darwin 1859) and that diverse communities should be more resistant to invasion than less diverse ones (Elton 1958).

Phylogenetic diversity of non-native plants on remote islands reflects introductions as the main driver of non-native plant diversity rather than speciation (Fig. 12.1). A recent assessment of pre- and post-European colonization of six southeastern Pacific islands calculated an increase in phylogenetic diversity over time as a result of non-native plant introductions (Carvalho and Castro 2017). Due to the great variety of human-mediated dispersal pathways and motivations for introducing plants, the non-native component of island floras is today often more phylogenetically diverse than the native component (Hulme et al. 2008; Weigelt et al. 2015). With ongoing non-native introductions, island floras will come to more completely represent the global phylogenetic diversity of the world's plant species (Fig. 12.1).

The future diversification of non-native lineages is so far largely unknown, although a growing number of studies are reporting interspecific hybridization and rapid evolution that may facilitate speciation (Felker-Quinn et al. 2013; Thomas 2015; Vallejo-Marin and Hiscock 2016; Morais and Reichard 2018). Following a human-mediated introduction, genetic isolation of invaders on islands could eventually give rise to new endemic taxa, with the process of speciation potentially accelerated by small founding populations subject to genetic drift and rapid adaptation to their novel island environment (Hendry et al. 2007; Schlaepfer et al. 2011; Stuessy et al. 2014). Hybridization introduces an avenue for rapid adaptation and potential speciation involving non-native lineages and may include crosses between two non-native species or between non-native and native species. Hybrid speciation is far more common in plants than animals, and it has been hypothesized that hybridization where at least one parent was transported by humans, may be the mechanism for most future plant speciations (Thomas 2015). For example, hybrid *Mimulus* species have formed instantaneously multiple times from parents originating from North and South America, forming stable populations outside of cultivation in Scotland and the Orkney Islands (Vallejo-Marin et al. 2015). Given the diversity of lineages currently being introduced to islands, speciation by hybridization provides a mechanism to integrate genetic material between early and newly established lineages, and conservationists on islands have raised concerns about the conservation of endemic species gene pools (Francisco-Ortega et al. 2000; Darwin et al. 2003). Although likely not as immediate as hybridization, speciation may eventually arise due to geographic isolation and genetic differentiation of populations on or within islands. Montesinos et al. (2012) provided a continental example of rapid evolution by revealing reduced seed viability for crosses between knapweed (*Centaurea* sp.) from its native European range and its invaded North American range in Europe, demonstrating a partial reproductive barrier. Other studies have found genetically based changes in defenses and traits thought to affect

competitive ability between native and invaded ranges, although none have addressed eventual speciation or adaptive radiation of human-mediated introductions on islands (Schlaepfer et al. 2011; Felker-Quinn et al. 2013).

12.2.2 Naturalization and Invasion

Naturalized Species Richness Is Higher on Islands

Similar to how island endemics represent a disproportionately high amount of Earth's total native plant richness despite their small size (Kier et al. 2009), an analogous trend exists for naturalized plants on islands. Multiple studies comparing ratios of non-native to native species richness per area show that the non-native proportion is higher for islands than continents, providing evidence for the claim that islands are more prone to plant invasion (Lonsdale 1999; Pyšek and Richardson 2006; van Kleunen et al. 2015b; Guo et al. 2017; Pyšek et al. 2017). In a database containing nearly 14,000 naturalized taxa from over 1000 regions, islands host 8019 of the total species, and more than 40% of island floras are composed of at least 40% non-native species (Pyšek et al. 2017; van Kleunen et al. 2019). Furthermore, investigating the relationship between area and naturalized species richness has revealed that islands show a steeper accumulation of non-natives with increasing area in comparison with mainlands. The fact that oceanic islands host more naturalized plants than equivalent mainland regions suggests that either something unique about island ecosystems encourages naturalization, and/or more species are introduced to islands, or species that are introduced to islands are somehow more invasive (Lonsdale 1999; van Kleunen et al. 2015b).

The question of why islands appear to be more invisable than mainland regions has been thoroughly discussed, although incompletely answered. Temperatures in maritime environments along island shores tend to be moderate relative to more extreme temperatures typical of many mainland areas, and it is possible that less extreme temperatures allow a wider range

of plants to survive and establish on islands, relative to mainlands (González-Moreno et al. 2014). Similarly, the land-ocean interface creates a large ratio of edge-to-interior habitat on islands, and edge habitats may be more susceptible to invasion. Biotic factors might also directly contribute to higher invasion rates on islands. As previously alluded to, a longstanding idea is that islands have more naturalized species because they are low in native species diversity, reflecting low natural immigration rates due to geographic isolation. Interestingly, non-native richness on islands appears to be positively correlated with distance from the mainland (Daehler 2005; Guo 2014; Pyšek et al. 2017; Moser et al. 2018), exhibiting the opposite pattern for native species, for which richness decreases with isolation. This pattern suggests that islands may accommodate more species due to the undersaturation of their biotic communities, which results in available resources or niches that can be exploited by new arrivals (Elton 1958; MacArthur and Wilson 1967). However, Lonsdale (1999) showed that despite islands having a higher proportion of non-native species than continents, there was no difference in the number of native species per area sampled, suggesting that low native species richness is not the general mechanism behind the high invasibility of islands, although low phylogenetic diversity on islands may still be a factor. Furthermore, the number of non-native species added to islands so far appears to not be correlated with the number of plant species that have gone extinct. These findings suggest either that a species saturation point has not been reached (or does not exist) or that these islands are accruing an “extinction debt” due to a lag time between introductions and future extinctions in response to those introductions (Sax and Gaines 2008; Kuussaari et al. 2009). It appears that far fewer extinctions have occurred for native plants than for animals, emphasizing the importance of monitoring to determine whether plants are less prone to extinction or if plant extinctions are merely delayed relative to extinctions in other taxonomic groups.

Introduction Effort

Perhaps the most conspicuously lacking information regarding plant invasions on islands is the number of species and individuals introduced (Tye 2006; Diez et al. 2009; Lockwood et al. 2009; Blackburn et al. 2020). The conclusion that islands are more invulnerable than continents assumes that introduction rates and propagule pressure have been similar for islands and continents, but a rigorous test of this hypothesis would require both a record of species that were introduced and the frequency of their introductions. Although a historical survey of horticultural resources, seed catalogues, and import records can sometimes be used to inform which species have been introduced (i.e., colonization pressure) (Daehler 2006; Sax and Gaines 2008), quantifying historic introduction effort for each species (i.e., propagule pressure) is more difficult. Invasion success is often bolstered by a large number of plantings (Colautti et al. 2006), as demonstrated in studies of escaped forestry species worldwide (Richardson 1998), and New Zealand flax (*Phormium tenax*), which was introduced in large numbers for the production of fibers on St. Helena and is now considered a troublesome invader (Cronk 1989). One study comparing non-native plants in the flora of Taiwan (near a mainland) and Hawaii (isolated from a mainland) found more naturalized species in Hawaii, with around half of this effect being attributed to greater susceptibility of Hawaii to invasion, suggesting that greater propagule pressure also contributed to naturalization of more species in Hawaii than in Taiwan (Daehler 2006). A comparison of New Zealand and Australia, which uniquely considered both naturalized and introduced species (failed naturalizations), showed that the probability of naturalization in New Zealand was not significantly different than in Australia, although New Zealand had more naturalized species richness per area (Diez et al. 2009), which may be explained by differences in the number of species introduced. While additional studies are needed, it is possible that high islands with large human populations experience more introductions and/or higher propagule pressure per unit area than mainlands.

A global assessment revealed that species of direct value to humans (e.g., edibility) are over-represented in the naturalized floras on islands (Pyšek et al. 2017). Future studies may reveal that islands experience more intentional introduction effort (per unit area) for food plants and ornamental plants, especially when native island floras have limited diversity. A high proportion of naturalized or invasive species has been introduced as ornamentals in Hawaii, Puerto Rico, the Virgin Islands, and New Zealand, which points to horticulture as playing an important role in plant naturalizations via the repeated introduction and propagation of popular species (Buddenhagen and Timmins 1998; Daehler and Carino 1999; Rojas-Sandoval and Acevedo-Rodriguez 2015). Understanding historic human motivations and current attitudes toward introduced plants on islands in comparison with continents could help illuminate whether people are (or previously were) more likely to introduce plants to islands and which species might be imported (Daehler 2006).

Do Native Island Floras Provide More Opportunities for Invasion?

Many have suggested that island natives are less able to resist invasion regardless of their richness, pointing to their evolutionary history and associated traits as more important in determining an island's invasibility than the number of natives present (Elton 1958; Simberloff 1995; Lonsdale 1999; Denslow 2003). Due to limited numbers of colonists naturally arriving on islands (especially remote islands), much of the genetic diversity may be derived from a few colonists, resulting in particular taxonomic groups and functional traits being underrepresented or absent in the native flora. For example, the lower elevation of tree lines on islands in comparison with mainlands of the same latitude may be explained by fewer tree species on islands that can tolerate extreme conditions, especially low temperatures found at the highest elevations (Karger et al. 2019). However, ecological adaptations lacking in the native flora may be present in introduced plants, providing opportunities for invasion with minimal competition from resident species. For instance, Kueffer

et al. (2009) uncovered gaps in fleshy fruit traits (size, nutritional quality) among native species that are now filled by non-native plant species, giving them dispersal advantages and facilitating their invasion on the oceanic island of Mahé (Seychelles, Indian Ocean). More broadly, some families and genera are disproportionately represented by naturalized plants on islands in comparison with mainlands, and some species, e.g., papaya (*Carica papaya*) and mango (*Mangifera indica*), are more likely to be reported as naturalized on islands than on continents (Pyšek et al. 2017). These findings invite questions about whether non-native taxonomic dissimilarity on islands and mainlands is the result of different taxa being dispersed by humans or whether certain lineages are more likely to find empty niche space on islands than elsewhere.

In comparison with mainland lineages, the evolution of endemic island lineages often occurs in the absence of diverse competitors, predators, and diseases, establishing island floras as not only phylogenetically simplistic but ecologically naïve (Denslow et al. 2009; Caujape-Castells et al. 2010). Furthermore, some studies have found that invasive species are more likely to originate from regions with high plant phylogenetic diversity, while regions with low phylogenetic diversity are comparatively more invaded (Fridley and Sax 2014; Saul and Jeschke 2015). These hypotheses are particularly relevant for islands because the “evolutionary naïvete” of island endemics may put them at a disadvantage relative to mainland species that have evolved to survive with a greater diversity of antagonistic interactions (Fridley and Sax 2014). Additionally, invaders of islands may benefit from comparatively fewer predators or diseases in comparison with their native communities (i.e., “enemy release”), which may bolster population growth (Catford et al. 2009). The idea that islands are more invulnerable due to naïvete or the low probability of encountering enemies is supported by the observation that most problematic invaders on islands come from mainland floras rather than other island floras (Kueffer et al. 2010). Similarly, island species rarely invade continents, although a small number of exceptions exist (Fridley and

Sax 2014). Non-native richness on islands also appears to be positively correlated with distance from the mainland (Daehler 2006; Guo 2014; Pyšek et al. 2017; Moser et al. 2018), while native species richness is negatively correlated with isolation, and importantly, remote islands are very often comprised of mostly endemic species derived from a small number of lineages. Thus, more non-native species appear able to establish among highly specialized endemic floras on remote islands, while naturalization may be less likely when introductions encounter less-isolated biotas.

The Role of Habitat Disturbance

Human-caused habitat disturbance appears to be strongly correlated with the naturalization of non-native plants on islands because numerous proxies of disturbance have been associated with increases in non-native species richness, including *per capita* gross domestic product (GDP), tourism, and human population size and density (Chown et al. 2005; Denslow et al. 2009; Kueffer et al. 2010). It has been suggested that the trend of disproportionately high naturalizations on islands may be due to islands being more disturbed by humans, and Kier et al. (2009) reported that measures of human impact are significantly greater for islands than mainlands. Additionally, Dawson et al. (2017) found that non-native species richness for multiple taxonomic groups is more strongly correlated with GDP for islands than for mainland regions, further suggesting that alteration of habitat caused by humans may be a significant factor promoting patterns of non-native plant diversity across islands. However, GDP may also reflect higher plant introduction rates, especially among ornamentals, resulting in higher naturalization rates for islands than for mainland regions.

Although spatial patterning and severity of habitat alterations have not been comprehensively assessed across a large sampling of islands, many have undergone intensive human disturbance, especially islands with sufficient area and elevational range to provide resources such as freshwater and arable land (White et al. 2007; Kueffer et al. 2010). As the availability of these

human-valued resources appears to coincide with factors that also determine native species richness (e.g., elevation, island size), it is likely that islands that host the most diverse native floras will also be highly attractive for human habitation and land transformation. On large islands, intensive agricultural disturbance regimes have converted many lowland habitats to non-native-dominated ecosystems, while intact native ecosystem fragments are often relegated to higher elevations (Macdonald et al. 1991; Caujape-Castells et al. 2010; Kaiser-Bunbury et al. 2010; Mueller-Dombois and Fosberg 2013). However, major habitat alterations from non-native ungulates such as goats and pigs are common threats to high-elevation ecosystems on tropical islands. Multiple authors have shown that non-native plant species richness tends to be highest at low-mid elevations on islands, with some suggesting that this may be at least partially due to the fact that these areas also overlap with greater degrees of human disturbance as well as major sites of introductions on islands (Macdonald et al. 1991; Tassin and Riviere 2003; Arévalo et al. 2005; Pauchard et al. 2009; Paudel et al. 2017; Steinbauer et al. 2017).

Nested Patterns of Invasion Between Islands

Most knowledge about broad biogeographical trends of non-native plants on islands has been garnered from studies comparing numbers of species between landmasses, while studies accounting for which species contribute to these patterns are rare. Important exceptions are analyses that have uncovered nested patterns of non-native plant species for both regional and global analyses of island floras (Greve et al. 2005; Traveset et al. 2014). Based on the analyses of common and dominant invaders, Traveset et al. (2014) found that small islands tend to be invaded by species that also invade larger islands. This pattern reflects differences in habitat availability, where small islands contain a fraction of habitats from large islands and thus can support a subset of the non-native species found on larger islands. Additionally, islands that have widespread invaders were found to most likely host species that

exclusively invade single or few islands, and the least invaded islands tended to be invaded by species that are common invaders elsewhere. These nested patterns of species reveal that some proportion of species are widely transported globally and regionally across islands (Greve et al. 2005; Traveset et al. 2014), but importantly, a large fraction of invaders (63% of the 350 species in the analysis by Traveset et al. (2014)) are found on a single island or island group. Additional studies are needed to investigate whether the prevalence of single-island invaders reflects the biotic conditions or anthropogenic history of islands or whether they are comparatively recent introductions that have not yet spread to other islands (Traveset et al. 2014).

12.2.3 Impacts

Are Impacts Stronger on Islands?

The assumption that islands are more vulnerable to plant invasions than continents is based on the observation that the non-native proportion of floras is higher for islands, but whether impacts per invader are greater on islands remains unclear. In general, impacts of invasive plants are not well documented and are difficult to measure (Hulme et al. 2013), although changes to ecosystem dynamics have been demonstrated through case studies on soil erosion, nutrient cycling, fire regime, hydrology, and seed dispersal (Vitousek et al. 1987; D'Antonio et al. 2000; Heleno et al. 2013; Meyer 2014; Downey and Richardson 2016). Meta-analyses of plant invader impacts have explored differences between islands and mainlands with respect to a variety of invader impacts, including changes to animal and plant communities as well as fire regimes and soil characteristics (Vilà et al. 2011; Pyšek et al. 2012). Pyšek et al. (2012) report a clear distinction between islands and continents, with invasions on islands more likely to result in significant impacts to plant and animal richness. In fact, a significant impact of invaders on local richness was found on all islands studied, regardless of ecosystem type or invader traits. Contrastingly, invasions on continents only impacted animal

richness in 31% of studies, and impacts to plant communities were highly dependent on invader characteristics. Additional data are needed to determine whether the magnitude of impacts is related to island remoteness and isolation. A general issue with meta-analyses of invader impacts is that they are based on a nonrandom sample of invaders; if a small fraction of naturalized species has inherently higher impacts regardless of their invasion on continents or islands, then islands may be more likely to harbor such high-impact invaders simply because they have more naturalized species. One approach for assessing impacts that avoids these issues is to compare impacts of the same invaders in island versus continental settings.

The few studies that have contrasted impacts (or proxies for impacts) of the same species on comparable island and mainland regions have yielded mixed results. A comparison between islands and continents in the western Mediterranean revealed that the weedy herb, Bermuda buttercup (*Oxalis pes-caprae*), occurred more frequently on islands and was present in more habitats than on the mainland, although abundance did not significantly differ (Gimeno et al. 2006). Under the assumption that impact intensity is a function of both distribution and local abundance, it was estimated that the intensity of impacts on the islands was approximately twice that on the continent. However, this effect may partially be due to greater human disturbance on islands rather than islands being inherently more vulnerable to impacts, considering that *O. pes-caprae* dispersal is aided by human and domestic animal disturbance, which were more prevalent on the sampled islands. Zenni et al. (2019) provide a comparison of invader performance and competitive effects between a continent (Brazil) and a remote island (Hawaii). The widespread invasive grass, molasses grass (*Melinis minutiflora*), outperformed native species from both regions in a greenhouse setting, but the biomass of island natives was less negatively impacted than continental natives, contradicting the idea that island species are more vulnerable to invader competitive effects (Zenni et al. 2019). More comparative studies are needed

to determine whether competitive impacts of invaders are greater on islands and whether mechanisms of impact are different than on continents, especially in tropical regions for which competition studies are particularly depauperate (Barton and Wong 2019).

Relative to continents, impacts of plant invaders on islands may be more strongly mediated by third parties, such as introduced animals, diseases, and mutualists (Box 12.1). These non-plant introductions may dramatically enhance or accelerate competitive impacts of plant invaders, resulting in larger apparent impacts on islands, relative to continents. Human-introduced non-plant species on islands often facilitate the spread and increase the abundance of invasive plants (Simberloff and Von Holle 1999). For instance, multiple invasive bird

species are known to disperse the fleshy fruits of problematic plant invaders on islands and may simultaneously be increasing germination rates due to removal of the fruit pulp, amplifying the impacts of plant invaders (Williams and Karl 1996, 2002; Mandon-Dalger et al. 2004; Gosper et al. 2005; Williams 2006; Heleno et al. 2013). Other non-plant mediators cause disturbances that weaken native plants, including non-native ungulates and diseases. These impacts involve two steps: (1) when a non-plant agent removes a portion of the native vegetation, either by herbivory, trampling, or dieback from disease, and then (2) when non-native plant species regenerate more quickly than native species, disrupting natural succession processes, resulting in a markedly different ecosystem. Studies of feral pigs on islands,

Box 12.1 Laysan Island

The story of Laysan Island represents an extreme but nonetheless representative example of non-native plants on islands and their complex interaction with humans and other introduced species. At the turn of the twentieth century, commercial enterprises were established to harvest the guano as well as eggs and feathers from dense seabird colonies on Laysan. Rabbits were subsequently introduced as pets and for food, which proliferated and denuded the island within two decades. The vacuum left by the depleted vegetation was shortly filled by non-native plants, such as spiny sandbur grass (*Cenchrus echinatus*), which degrades the quality of nesting habitat (Flint and Rehkemper 2002). Intensive habitat restoration efforts have occurred within the last few decades, requiring invasive plant control programs alongside the reintroduction of closely related substitutes of extirpated species. For example, it is unknown whether the *Pritchardia* palms that once lived on Laysan were *P. remota* or a unique species, yet individuals of *P. remota* from nearby Nihoa island have been introduced to possibly fill their role. Additionally, endangered Nihoa millerbirds have been introduced to replace a now-extinct Laysan subspecies and establish a second population in hopes to prevent extinction (Farmer et al. 2011).

Top: Artist depiction of Laysan island in the 1800s' showing nesting birds among native vegetation, with species composition based on photos and field notes taken in 1896 (Schauinsland 1899) as well as pollen and seeds identified from sediment cores (Athens et al. 2007), including some extinct taxa: fan palm (*Pritchardia* sp.), Hawaiian chaff flower (*Achyranthes atollensis*), coastal phyllostegia (*Phyllostegia variabilis*), Laysan honeycreeper (*Himatione fraithii*), and Laysan millerbird (*Acrocephalus familiaris*) artwork by Jared Bernard

Middle: Photo of Laysan Island taken in 1923, two decades after the introduction of rabbits, showing almost complete removal of vegetation (photo by Alexander Wetmore on the Tanager expedition, archived by the Smithsonian Institution).

Bottom: Laysan Island in 2006 with nesting albatross after restoration efforts, including the re-introduction of *Eragrostis variabilis*, a native bunchgrass that restabilizes the soil and promotes nesting habitat (photo by Cindy Rehkemper, USFWS)



for example, show that while these ungulates suppress growth and recruitment of both native and non-native species, non-native plant recruitment may outpace native species after ungulates are removed (Weller et al. 2011; Cole et al. 2012). Likewise, canopy gaps arising from tree diseases may be more rapidly filled by non-native species, especially those that produce numerous, long-lived seeds (Cordell et al. 2009). Although the number of studies quantifying invasive impacts is growing (Hulme et al. 2013), these examples emphasize the need to consider how impacts are influenced by non-native assemblages comprising multiple trophic levels.

Biodiversity Change Over Time

Although we cannot conclude that an individual plant invader's impacts will be greater on islands than on continents, it seems logical to assume that net impacts of invaders on islands have been greater than on continents because islands have accumulated proportionally more non-native species. In addition to island taxa evolving alongside fewer competitors, predators, and diseases, one might guess extinction to be more prevalent on islands simply because island natives tend to have smaller populations that are more easily extirpated (Losos and Ricklefs 2009). However, few case studies exist documenting non-native plant invasions as a direct cause of extinction, and worldwide studies show that invasions have so far exceeded extinctions on islands, often by a large margin (Sax et al. 2002; Sax and Gaines 2008). This phenomenon has sparked much debate about the fate of biodiversity on islands. The current lack of data linking invasive plants to widescale extinctions is often contrasted with animals and diseases, which provide the bulk of the empirical evidence supporting claims that invasive species are a major threat to global biodiversity (Russell et al. 2017). Contrarily, invasive plants may contribute to extinctions in nuanced ways that are difficult to detect. For example, hybridization between native and non-native plants has likely been occurring for decades without detection, as is the case for the Galapagos endemic *Gossypium darwinii* G. Watt, where no pure populations can be confidently

identified due to widespread crossing with cultivated cotton (Daehler and Carino 2001). The threat of hybridization has also been documented on islands for a few other endemic species, including *G. tomentosum* Nutt. ex Seem. and *Arbutus canariensis* Veil., which are found only in the Hawaiian and Canary islands, respectively (Levin et al. 1996). Moreover, several studies have reported reduced local population sizes or diversity associated with plant invasions, but understanding how these declines affect extinction risk for an entire species is more difficult to determine (Weller et al. 2018). Given that many generations are necessary for invaders to reach their full range and density, and several decades might elapse until the last individual of a native species dies, additional extinctions will likely be realized over time, with islands accruing "extinction debt" as invaders spread and become increasingly abundant (Sax and Gaines 2008; Kuussaari et al. 2009; Gilbert and Levine 2013; Downey and Richardson 2016).

One method of investigating the impacts of non-native additions on biodiversity is to measure biotic homogenization, where native species extinctions and/or the introduction of widespread species results in a locality or region becoming less taxonomically distinct. Despite the small global area comprised by islands, comparatively high rates of endemic species extinctions and non-native introductions stand to make them a disproportionate driver of worldwide homogenization, even if plant invasions are not the direct cause of island extinctions (Castro et al. 2010; Caujape-Castells et al. 2010; Pouteau and Birnbaum 2016; Gray 2019). At local or regional scales, however, non-native species may contribute to either homogenization or diversification, depending on whether they have spread widely or are localized and whether colonizations outnumber extinctions (Vergara et al. 2011; Rosenblad and Sax 2017).

Only a handful of studies have investigated floristic homogenization on islands, and although these analyses represent a range of spatial scales, each describes a unique pattern of floristic change, preventing a unified conclusion regarding homogenization on islands (Castro et al.

2007, 2010; Lambdon 2008; Shaw et al. 2010). A fourfold increase in the similarity between pre- and post-European species composition was detected among archipelagos across the Pacific and Atlantic Oceans (Castro et al. 2010), whereas comparisons of islands in the Southern Ocean, which have relatively lower human activity, revealed divergence among islands rather than homogenization (Shaw et al. 2010). A smaller-scale comparison of species among six islands in the southeastern Pacific revealed a slight trend toward homogenization (Castro et al. 2007), while Lambdon et al. (2008) found no difference in between-island and between-habitat similarity among non-native and native floras over time on islands in the Mediterranean. However, one important consistency that emerged from all analyses is that plant invasions have so far been a larger driving force behind local and regional biodiversity change than native plant extinctions. These results may suggest that plant invasions on islands are not inherently homogenizing, especially at smaller spatial scales, and that biotic changes that concern conservationists (i.e., declining native species and increasing non-native richness) do not necessarily result in net biodiversity declines (Vellend et al. 2017). Ultimately, a picture of biotic homogenization, where winning species of the Anthropocene become omnipresent while losing species disappear everywhere (McKinney and Lockwood 1999), is not currently supported by empirical evidence, although some case studies demonstrate disappearance of unique native species from specific islands, and many have argued that an “extinction debt” due to invasions has not yet been realized (Kuussaari et al. 2009; Gilbert and Levine 2013). For instance, conservationists often identify invasive plants as the main driver of population decrease leading to possible extinction, with certain species being particularly problematic (Meyer 2000, 2004).

Although we can conclude that plant invasions have not been balanced by native plant extinctions on islands, there are different explanations for this pattern beyond the hypothesis of extinction debt. In some cases, native and invasive plant ranges may not overlap, precluding the possibil-

ity of plant invaders causing extinction directly, which may occur often on islands that have undergone intensive human disturbances resulting in entirely novel non-native ecosystems. As many non-native plant species preferentially colonize disturbed habitats (Ackerman et al. 2017), some new introductions may establish solely in ecosystems that are already non-native dominated. This spatial separation of native and non-natives may partially explain why non-native plant richness is often positively rather than negatively correlated with native species richness across islands, especially if native ecosystem fragments remain large enough to prevent extinctions (Gilbert and Levine 2013). In addition to habitat separation, native and non-native plant populations on islands may coexist if the competitive superiority of invaders over native species is reversed in some proportion of available habitats or at particular sites within a shared habitat. Plant invaders often outperform native species only in certain environmental conditions rather than across all scenarios, and thus, it is feasible that some native species may be locally extirpated within part of their range while remaining competitively superior in other environments (Daehler 2003). This possibility seems especially likely on islands that exhibit dynamic differences in rainfall and temperature over very short distances, because assuming the native species is tolerant of some range of conditions, this provides a variety of environments within which competitive dynamics may vary (Diez et al. 2008).

Economy and Human Dimensions

While the impact of invasions on island biodiversity has been a key focus of research, impacts of plant invaders on island culture, economy, and human health are conspicuously lacking. These studies are urgently required for biosecurity planning and to identify human needs that may be unique to islands. Factors and circumstances that appear to promote vulnerability of native island ecosystems may also result in larger impacts of plant invaders on humans (Russell et al. 2017). For instance, in the same way that islands host a disproportion-

ate number of endemic species, the isolation of islands gives rise to unique human cultures; 27% of human languages are spoken exclusively on islands (Tershy et al. 2015). These cultures may be sensitive to impacts of plant invasions because the unique biota of island communities is often inextricably tied to cultural identity (Simberloff 2013; Russell et al. 2017). Similar to depauperate native biotas that evolved among fewer competitors and predators, less resilient economies are prevalent on islands, as they are often less diversified (Russell et al. 2017). Thus, invasive species that decrease the viability of particular industries may contribute substantially to economic instability and decrease revenue sources available to residents of islands more drastically than would be expected in larger mainland economies (Reaser et al. 2007; Russell et al. 2017). Island agriculture, for example, which may initially draw investment and establish practices based on an absence of many pests, may be strongly impacted by the arrival of new invasive plants that are weeds of crops or that provide alternative hosts for agricultural pests or diseases. The coinciding higher degree of endangerment of cultural aspects and economies on islands relative to continents evokes questions about whether similar processes that endanger native species reflect the endangerment of island cultures and economies. Islands may therefore be good candidates for integrated cultural and ecological approaches to conservation (Winter et al. 2018).

Impact Prediction on Islands

Given the high number of non-native plant species that have been introduced to islands, both cultivated and escaped, accurate prediction of their impacts is necessary to efficiently conserve island floras and protect island economies. Plant characteristics such as a history of invasion elsewhere, perennial life history, taxonomy (e.g., Fabaceae, Poaceae), and originating from similar climate can be useful indicators of problematic invaders on islands (Pheloung et al. 1999; Kueffer et al. 2010; Gordon et al. 2016). However, these

studies also point out a high degree of taxonomic and ecological diversity among island invaders, and importantly, problematic species on one island do not necessarily become problematic on all, or even most, islands where they are present (Meyer 2000; Kueffer et al. 2010). For instance, 10% of species consistently cause problems where they were introduced, while the rest only have done so in some cases. This pattern suggests that invasive plant impacts are context-dependent and likely depend on factors such as human activities and habitat conditions.

Weed Risk Assessment programs have been tested and/or implemented on islands to help inform importation decisions at borders and promote low-risk plantings (Daehler et al. 2004; Kato et al. 2006; Gordon et al. 2016). Many of these systems rely on information about the species being assessed, while factors such as island-specific human activities and habitat conditions remain difficult to incorporate. The Hawaii-Pacific Weed Risk Assessment (WRA), for example, contains 49 questions about a species' biology: the majority addressing the likelihood that a species will escape and spread (e.g., seed dispersal mechanisms), while a smaller fraction considers potential consequences of invasion (e.g., forms monotypic stands/thickets) (Daehler and Virtue 2010). As a result, the WRA provides a somewhat coarse assessment of impact potential, attempting to answer the question "Is this plant likely to cause impacts?" rather than "What might be impacted, and how bad will it be?" To address such questions, new risk frameworks are needed that can determine the type and magnitude of impacts on islands (Blackburn et al. 2014). In addition to assessing potential impacts of new non-natives, many non-native plants have already arrived and have become naturalized on islands, and managers need tools to help them prioritize management efforts among these species. Thus, the ability to rank species based on the magnitude of their potential impacts rather than a simple high- or low-risk rating is a necessary tool in these species-rich management scenarios and would be especially valuable if paired with a framework to estimate control or eradication feasibility (Kriticos et al. 2018). To this end,

the IUCN (2018) has proposed guidelines for managing invasive species on islands that emphasize the value of feasibility assessments.

Recent protocols for assessing impact potential have been proposed where the resource consumption of candidate non-native species is measured against similar (analogue) native species, thereby calculating a score that can be compared among species to determine which non-natives might have the most impact (Dick et al. 2017; Dickey et al. 2018). While these methods show promise for predicting harmful invaders that have no invasive history and are enticing in that they allow comparison of multiple species, these approaches may have limited practical applicability on remote islands, where there is often no information available on resource uptake rates of endemics relative to non-natives. Also, some non-natives have no analogous endemics, although some contend that lack of a native analogue alone should signal the potential for high impacts (Dick et al. 2017). Further research addressing whether species traits that increase the likelihood of invasion are correlated with the ability to inflict greater impacts could assist with prioritization, especially on islands that have already accumulated plant trait and impact information in weed risk assessment databases (Levine et al. 2003; Pyšek et al. 2012). Supplementing existing weed risk assessment frameworks by incorporating island-specific factors such as disturbance regimes, propagule pressure, and an understanding of their often unique endemic habitats may be a cost-effective avenue for enhancing the predictive power of impact assessments. Implementation of schemes such as the Environmental Impact Classification for Alien Taxa (EICAT), which classifies species according to five impact categories, could be useful for management prioritization of invasive plants on islands (Blackburn et al. 2014; Hawkins et al. 2015). Although this scheme is not intrinsically predictive because it rates species based on their impacts elsewhere, widespread usage will allow comparison of impacts between islands, providing a springboard for the development of quantitative or semiquantitative prediction and prioritization tools.

12.3 Opportunities

12.3.1 Preventing Invasions

Invasive plant management strategies encompass prevention, eradication, and control, which roughly reflect successive stages in the invasion process: introduction, establishment, spread, and increasing impact (Hulme 2006). The geography of oceanic islands provides a unique opportunity to prevent potential invaders from introduction, as their lack of terrestrial borders restricts the introduction of land-dwelling species to a few ports of entry. Multi-island countries or states may further exploit this opportunity by using natural oceanic borders to define management areas and implement biosecurity strategies to contain problematic invaders to single islands (Russell et al. 2017). Furthermore, islands tend to be small in area, increasing the opportunity for early detection and intervention to eradicate unwanted introductions. Accordingly, most successful eradications have occurred on islands (Myers et al. 2000). The comparative cost of managing invasive plants once they establish has led many to emphasize the prevention of arrivals as the most beneficial and cost-effective strategy (Leung et al. 2002; Hulme 2006). However, sophisticated biosecurity plans are necessary to take advantage of unique features of island geographies, particularly for multi-island zones for which nested strategies are needed to prevent introduction as well as interisland spread. These biosecurity plans, when present, are currently highly diverse and implement a wide range of strategies dependent on governance and economics (Cook et al. 2010; Heikkilä 2011). Island territories sometimes fall under the auspices of continental biosecurity plans, presenting a special problem, as regulations that were designed to protect mainland environments and economic interests may not be appropriate for islands; for example, island territories may have different climates from politically affiliated mainland areas and benefit from a different list of species to exclude from entry (Quinn et al. 2013). Additionally, an island may require more strin-

gent biosecurity than a mainland area because of differing susceptibility to invasion.

While islands hypothetically lend themselves to preventative or early intervention strategies, many factors may complicate pre-border screening or post-border eradication for small populations. Some islands of high conservation value still have few or no invaders; these are mostly small islands with few or no human inhabitants for which border biosecurity is both important (Oppel et al. 2019) and easy to implement because of rare human visitation and a general support of biosecurity procedures by island stakeholders. Examples are Palmyra Atoll and the Northwest Hawaiian Islands. Access is only by ship, all visitors require permits, and strict procedures have been established to ensure that no seeds are accidentally brought to the islands by visitors. An effective exclude-all approach to biosecurity becomes less feasible on islands with more human residents and visitation. In these situations, practical implementation of effective prevention and early intervention procedures requires the ability to accurately separate invaders from non-invaders, with assessments especially being needed of potential magnitude of harm and control feasibility, in order to prioritize detection and eradication programs. As these tools have been generally lacking, comprehensive “blacklists” and early detection survey lists attempting to account for the high degree of uncertainty underlying invasion impact prediction may become large and unwieldy, while oversimplified lists may provide a false sense of security (Hulme 2006). Managers cannot merely rely on accounts from invasions elsewhere, as studies recognizing the prevalence of single-island invaders worldwide demonstrate that addressing threats from only the most widespread species could potentially ignore very problematic new invaders (Kueffer et al. 2010; Traveset et al. 2014). Another important challenge is that many islands already host a significant number of non-native plant species that are in various stages of the invasion process (Kueffer et al. 2010); in these circumstances, ongoing control efforts can attract more attention and resources than prevention, even if greater investment in border security

would more effectively reduce invader impacts over the long term. While it is generally recognized that border security requires the employment of agents to monitor entry points, which are mainly restricted to ports and airports on islands, and the public generally understands that some organisms may be denied entry to islands due to biosecurity procedures, an effective biosecurity program also requires support from taxonomic experts to ensure accurate identification of organisms detected during biosecurity protocols. The taxonomic support and expertise required for pre-border inspection, as well as for post-border field surveys and to conduct risk assessments, is likely an expense that is not well appreciated, especially for tropical islands (Hulme 2006). Established institutions that already collect and curate plant biodiversity data, such as herbaria and botanical gardens (who often show interest in island floras), may be co-opted or supplemented to reduce the cost of these needs. Additionally, automated plant identification using artificial intelligence is a promising technology that could help reduce the workload and expertise involved in identifying thousands of specimens at borders and could be further leveraged with crowd-sourced identifications from citizen science platforms (Wäldchen et al. 2018).

The decision to emphasize pre-border versus post-border management of non-native plants may depend on the introduction pathway for the plants (Carrasco et al. 2010; Moore et al. 2010; Rout et al. 2011). For instance, border prevention may be the most effective strategy for popular ornamental species that have been designated as regulated pests. Post-border regulation of such plants is less likely to be effective because once introduced into the horticultural trade, these plants have many avenues to disperse widely and quickly across an island, often to private lands which may be difficult to search, and eradication attempts may lead to conflicts with plant owners. On the other hand, relying on pre-border measures for islands that are already heavily invaded will likely miss opportunities to prevent environmental or economic losses through eradication of established species. Furthermore, the arrival of certain new introductions may not add substan-

tial harm beyond that already caused by established invaders (Morais et al. 2017), so an understanding of established invaders and their impacts can feedback on pre-border biosecurity decisions to maximize the efficiency of resource allocations. A balance of prevention, eradication, and control strategies is needed, although the proportion of funding and resources that should be allocated to each strategy is island-specific and complicated for islands that experience frequent invasions (Rout et al. 2011). Multispecies tools to assess the tradeoffs between management approaches (e.g., the future impacts of known, established invaders versus the unrealized potential impacts of preventable invaders) are urgently needed to support these decisions, especially those that can contrast likely impacts among species and quantify uncertainty in limited budget scenarios (Carrasco et al. 2010).

When the number of individuals is limited, plant invasions may be prevented by eradication, with the feasibility of this method proven by a growing list of success stories (Kraus and Duffy 2010; Smith-Ramirez et al. 2017; Simberloff et al. 2018). Although quantifying the future costs of invasion (including nonmonetary impacts) is very difficult, the cost of control later, should a species become a problem, is likely to be many times higher than eradication (Rejmánek and Pitcairn 2002; Burnett et al. 2007; Moore et al. 2011). For example, a program in the Galapagos designed solely to tackle small populations of incipient species revealed that many eradications could be completed for a relatively low cost (e.g., <10,000 USD) (Buddenhagen and Tye 2015). However, an extensive assessment of feasibility is required to avoid tackling species that are beyond eradication, and recognizing common pitfalls is crucial for success (Cacho et al. 2006; Panetta et al. 2011; Hulme 2020). Chief among these issues are the lack of recent species inventory and distribution data, which may cost more to obtain than the eradication cost itself but are crucial to avoid a long and costly program that never achieves its goal (Cacho et al. 2006, 2007; Panetta and Cacho 2012). Most reports of new naturalized species are made by people with formal botanical training, empha-

ing the need for technical skills to identify unfamiliar species (Hosking et al. 2004). Additionally, eradication programs often require multiyear commitments, and inability to make such commitments due to waning interest or funding instability contributes to program failures (Panetta et al. 2011; Buddenhagen and Tye 2015; Simberloff et al. 2018; Hulme 2020). Invasive species management programs on islands with human settlements or resources used by humans are complicated by the need for public support, especially if infestations occur on private lands, and in many instances, landowner permission can make or break an eradication attempt (Glen et al. 2013; Buddenhagen and Tye 2015; Niemiec et al. 2017). Conducting control efforts for multiple species simultaneously is evidently a common task for conservation organizations on islands (Kueffer 2010; Glen et al. 2013), emphasizing the need for tools to help prioritize species for eradication (Panetta et al. 2011; Panetta and Cacho 2012).

12.3.2 Restoration and Control for Established Species

Many control programs have been implemented on islands, encompassing a variety of chemical and biological methods to contain invasive populations or restore invaded areas. Although the smaller area of islands may simplify management efforts compared to larger areas on mainlands, case studies from islands demonstrate that control programs are nonetheless costly endeavors (Meyer 2014; Smith-Ramirez et al. 2017). For example, feasibility assessments revealed that approximately ten million USD would be needed to control Ceylon raspberry (*Rubus niveus*) on Santiago Island in the Galapagos, of which approximately 100 ha is infested of its 585 km² total area (Renteria et al. 2012).

As many inhabited islands are highly modified and contain a large number of long-established invasive species, biological controls (biocontrols) are possible solutions for effective long-term management on islands. These methods are currently in place to manage numerous invasive plants on

islands, particularly woody species, and there are even some examples of eradications attributed to biocontrol agents (Smith-Ramirez et al. 2017). Modern biocontrol selection protocols utilize a phylogenetic-based approach to assess the probability that candidate enemies of invasive species could shift to attack related native species (Pemberton 2000). As the flora of remote islands is derived from few colonists, the biocontrol species selection process is theoretically easier on islands because closely related native species may be absent. For example, many problematic members of Melastomataceae have naturalized on islands, including the well-known invaders *Miconia calvescens*, *M. crenata*, and Koster's curse (*Clidemia hirta*). However, many western Pacific islands have no native Melastomataceae because the family's center of diversity occurs in continental South America (dos Santos et al. 2012), allowing conservationists to take advantage of candidate biocontrol species with comparatively broad host ranges such as *Ditylenchus gallaeformans*, a family-specific (rather than species-specific) nematode being investigated for biocontrol of multiple Melastomataceae (Oliveira et al. 2013). Biocontrol efforts on islands may also benefit from comparatively simplistic trophic interactions. One study comparing the effect of biocontrol agents for *Lantana camara* showed that control and defoliation appeared higher on islands than on continents, with one possibility for this discrepancy being fewer predators on islands (Zalucki et al. 2007). Interestingly, Hawaii was an exception to the trend of higher defoliation by biocontrol agents on islands; this may be because hundreds of insect species have already been introduced there, including purposeful introductions of predators of agricultural insect pests (Henneman and Memmott 2001). For example, a tephritid fly introduced in Hawaii as a biocontrol for *L. camara* was attacked by a biocontrol wasp introduced to control a different tephritid fly pest of agriculture (Duan and Messing 1999), rendering the *L. camara* control agent less effective.

One of the greatest obstacles facing ecosystem restoration is the unpredictability of community dynamics after the removal of invasive species, given that the nature of interspecific interactions

is entirely unknown for many non-native species (D'Antonio et al. 2017). Long histories of intensive disturbance regimes combined with a plethora of non-native plant species on many islands have resulted in an abundance of highly modified ecosystems (Box 12.1). Restoring ecosystems to a pre-human state may be infeasible for "novel ecosystems" dominated by non-native species, which is often the case for lowlands that have historically been cleared for agricultural purposes (Hobbs et al. 2006, 2009; Kueffer and Daehler 2009; Meyer et al. 2015). Variation in restoration outcomes may in part be due to the amount and types of resources available, which vary widely across ecosystems on islands. For example, D'Antonio et al. (2017) recently summarized their findings from multiple removal experiments on Hawaii Island, revealing complex patterns of species recruitment. Removal of a dominant non-native grass species from mesic forests resulted in a flush of a secondary non-native species, whereas this did not occur in a lowland dry forest. On the other hand, in light-limited lowland wet forests, removal of a dominant canopy invader led to invasion by a highly diverse suite of fast-growing species comprising species from a range of functional groups, rather than invasion by a single dominant species. Thus, it cannot be assumed that the removal of invasive plants will result in ecosystem recovery, and in some cases, control efforts may even promote invasion and incur a net negative outcome (Jäger and Kowarik 2010; Prior et al. 2018). Further studies are needed on "priority effects," the phenomenon where certain invaders suppress the establishment of species that arrive later, to understand when the removal of one invader may result in the establishment of another species that may be more impactful or harder to control (D'Antonio et al. 2017). Additional studies combining data on invader arrival timing and priority effects may help explain why widespread invasive species end up dominating some islands while failing to become problematic on others even after many decades of establishment (Kueffer et al. 2010).

Further complicating island restoration efforts is the generally lower native functional diversity of islands relative to mainland ecosystems. Out

of the pool of candidate species (non-native and native) that could potentially colonize a perturbed site, native flora may lack functional traits that are encompassed by non-native species (Ostertag et al. 2015; D'Antonio et al. 2017), increasing the probability that non-natives will be recruited (Funk et al. 2008). Although there are examples of resilience in native island ecosystems where native species recolonize after the removal of invaders (Loh and Daehler 2008; Jäger and Kowarik 2010), resource managers increasingly acknowledge that restoration of heavily disturbed ecosystems on islands may require conservation intervention in perpetuity. Given limited resources for the control of widespread and impactful species, invasive species managers often have the unfortunate task of subjectively choosing small natural areas most worthy of attention (e.g., critical habitat for endemics). An increased focus on multispecies control strategies should be considered, as plans emphasizing single species are unlikely to translate into native ecosystem restoration in scenarios where many non-native species are present (Glen et al. 2013). Ostertag et al. (2015) proposed selecting species for restoration based on functional traits, including the use of relatively inert (noninvasive) non-native species whose functional traits complement those of the native community. In lowland wet forests in Hawaii, their ongoing restoration project uses this method to increase community resistance to problematic invaders, and preliminary results showed high survival of native species in these “hybrid” native-non-native communities (Cordell et al. 2016).

12.4 Conclusion

The native biotas on remote islands have long fascinated both scientists and the general public. Yet, the oceanic obstacles that once prevented dispersal and generated uniqueness are now easily overcome by humans, who readily introduce new plant species for a variety of reasons. How introduced flora will influence the distribution of native flora and extinctions remains unclear, but the phylogenetic composi-

tion will certainly be altered given the differences between dispersal mechanisms for native and non-native species. Studies of biodiversity change are largely based on regional- or global-scale analyses of species presence/absence, and interestingly, the pace of non-native species introductions appears to so far be outpacing the extinction of native species, giving no indication that islands are approaching carrying capacity. However, these studies are unable to describe drastic species turnover in communities observed at the local level, and since extinction is likely a slow process (especially for long-lived species), it seems likely that extinction rates will accelerate for native species in the future as the impacts from invasions are realized. Range and population sizes must be monitored for both natives and invaders over broad geographic regions to gain a clearer understanding of plant biodiversity trends. Despite island borders theoretically lending themselves to preventative biosecurity efforts, the diversity and quantity of non-native species already present on some islands requires sophisticated management strategies. Conspicuous knowledge gaps exist regarding how human activities and preferences influence plant introductions and affect island and archipelago-level distribution and disturbance patterns. Ultimately, the plethora of non-native plants on islands presents conservationists with a biodiversity problem, whereby decisions regarding invasive plant management must consider assessments of relative impacts while also addressing interacting factors of disturbance and non-plant introductions that can lead to rapid declines of endemic island plants.

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Plant Invasions in Mountains

13

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Abstract

Due to extreme climate and limited accessibility, mountains are marked by low human population density and relatively little direct human interference. However, the recent anthropogenic footprint in terms of climate change, land-use changes, infrastructure developments, and increased global connectivity have made these pristine ecoregions more vulnerable to plant invasions. Mountain regions are undergoing rapid socioeconomic transformation, causing increased disturbances associated with infrastructure develop-

ment for transportation and tourism, changing the land use and land cover of these fragile landscapes. Climate change has emerged as an important factor that has the potential to accelerate the process of biological invasion in the mountains. Despite a large number of studies on mountain plant invasions, with some mountain regions being relatively well studied (e.g., European Alps) than others (e.g., Mountains of Central Asia), there is still a lack of information on the impacts of invasive alien plant species on these mountain communities. In this chapter, we review studies related to plant invasions in the mountain regions and discuss their drivers, pathways, patterns, and impacts. We also discuss the influence of climate change on plant invasions and finally discuss their management options. We anticipate the importance of future research on mountain ecosystems, including documentation of invasion patterns at varying spatial scales, and suggest further studies which could be useful in the management of invasive alien plant species.

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13.1 Introduction

13.1.1 Mountain Systems of the World

Mountain systems are widely distributed across the world. There have been several attempts, over the last few decades, to determine and map the mountain regions of the world (Kapos et al. 2000; Körner et al. 2011, 2017). The Global Mountain Biodiversity Assessment defines mountains as any land with a ruggedness threshold of more than 200 m asl elevation (Körner et al. 2011). Using this classification, an estimated 16.5 million km² or 12.3% of the land area are now considered as a standard figure for the global mountain area outside of Antarctica (Körner et al. 2011, 2017), with Asia having the largest area under mountains followed by North America, South America, Europe, and Africa and then the small fractions located in Australia, Greenland, and Oceania. This chapter reviews studies on plant invasions in mountain systems that include the Rockies of North America, the Andes in South America, the European Alps, Australian Alps, Kilimanjaro and Atlas in Africa, and Himalaya, Ural, Ghats, Pamir, Tibet, Kunlun, and Tianshan in Asia.

Mountains sustain nearly one-quarter of all terrestrial species diversity, host half of the 36 global biodiversity hotspots, and harbor many rare and endemic plant species (Vetaas and Grytnes 2002; Mittermeier et al. 2011; Noroozi et al. 2018; Habel et al. 2019). Mountains being the “water towers” of the world offer much of the global water supply that is so vital to human survival and the sustainability of all life on the planet. In addition to water, mountain ecosystems offer goods and services, including high-elevation medicinal plants, cultivated species, timber, and other forest resources (Schild 2008). Furthermore, mountains are rich in cultural heritage and traditions and provide diverse recreational opportunities (Schirpke et al. 2013). In addition, tourism and recreation play a significant role as they form the basis of local economies in many mountain

areas, often contributing significantly to the national economy (Fredman 2008). Unfortunately, these highly dynamic ecosystems are prone to loss of biodiversity due to their vulnerability to human and natural disturbances (Wang et al. 2018; Chakraborty 2021). Globally, mountain ecosystems are threatened by climate change, overexploitation, fragmentation, invasive species, etc. (Wang et al. 2019). Species in mountainous areas, for example, are already experiencing a range shift toward higher elevation due to increasing temperatures. Evidence shows that the spread of alien species in mountain regions affects the biodiversity of native species and has a negative impact on the economy and human health (Pauchard et al. 2009; Alexander et al. 2016; Lamsal et al. 2018). Hence, it is important to have a scientific understanding of plant invasions in mountain ecosystems. This review will provide general information on plant invasions in the mountain ecosystem, identify temporal trends and geographic biases in research, and provide a thematic focus on mountain plant invasions. It will also provide detailed information on patterns of invasive alien plant species (IAPS) richness along elevation gradients, introduction pathways and spread vectors, drivers of plant invasions, and their impacts and management in mountain areas.

Plant Invasions in Mountain Ecosystems

Mountain regions are often considered to be resistant to biological invasions (Pollnac et al. 2012). Because of extreme climate and limited connectivity, these regions have, until recently, been marked by low population density and limited anthropogenic activity. Low anthropogenic disturbances, low propagule pressure of pre-adapted species, and a steep elevation gradient probably explain why few non-native plants inhabit mountain environments as compared to the surrounding lowland ecosystems (Alexander et al. 2009, 2016; Pauchard et al. 2009; Carboni et al. 2018). However, as a result of climate change and increased global connectivity, mountain regions are now witnessing

rapid changes in terms of plant invasions. Over 200 non-native plant species have been recorded from the alpine environments around the world, although the Mountain Invasion Research Network (MIREN) database is limited to the mountain ecosystems of North America, South America, and Europe (Alexander et al. 2016). In recent years, some low-elevation species, including the pre-adapted IAPS, have shifted to higher elevations (Bradley et al. 2010; Alexander et al. 2011; Marini et al. 2013; Petitpierre et al. 2016), increasing competition for the native alpine vegetation (Diez et al. 2012; Sorte et al. 2013). Different factors, such as rapid evolution, phenotypic plasticity, propagule dispersal, habitat disturbance, and community invasibility, influence the spread and establishment of IAPS in mountain regions along elevation gradients (Pauchard et al. 2009; Kueffer et al. 2013; Alexander et al. 2016). Consequently, these invasive species are likely to have an increased impact on higher-elevation biodiversity in the near future (Pauchard et al. 2009; Alexander et al. 2016; Lembrechts et al. 2016; Petitpierre et al. 2016; Guo et al. 2018), in particular, due to intensification of human activities, climate change, land-use changes, human population growth, and tourism expansion (Kueffer et al. 2013; Pauchard et al. 2016). This may also have significant negative impacts on mountain biodiversity hotspots (Bellard et al. 2014). At least 100 IAPS, including *Acacia* spp., common broom (*Cytisus scoparius*), *Pinus* spp., *Salix* spp., oxeye daisy (*Leucanthemum vulgare*), silver cinquefoil (*Potentilla recta*), and common mullein (*Verbascum thapsus*), all deliberately introduced for pasture tree or ornamental purposes, have required management interventions in various mountain regions around the world (McDougall et al. 2011a). Despite all of this, mountain regions are still relatively free from alien species as compared to lowlands, so preventive actions could be an effective way for limiting future plant invasions in mountain regions.

13.2 Temporal Trends and Geographical Distribution of IAPS Studies in Mountains

To better understand temporal trends and present the geographical distribution of IAPS in mountain regions, we undertook a literature review using the Scopus database on publications produced between 2000 and 2019. The Boolean search string was used to retrieve publications on invasive plants from the database using keywords “mountain” OR “andes” OR “andean” OR “alps” OR “alpine” OR “Himalaya” OR “karakoram” OR “Hindu Kush” OR “ghats” OR “sierra” OR “serra” OR “macizo” OR “pamir” OR “Tibet” OR “TianShan” OR “Kunlun” OR “ural” OR “Kilimanjaro” OR “atlas” OR “Rockies” AND “Invasive plant” OR “Non-native plant” OR “Exotic plant” OR “Invasive Alien Plant” OR “Non-indigenous plant” OR “alien plant” OR “Alien flora” OR “Plant invasion” OR “Plant invader” OR “invasive weed.” This search identified 552 peer-reviewed articles. We used four time periods to look at the overall publication trend on IAPS, viz., (i) 2000–2005 (with a total of 65 articles, with an average of 13 per year), (ii) 2006–2010 (with a total of 145 articles, with an average of 29 articles per year), (iii) 2011–2015 (with a total of 166 articles, with an average of 33 articles per year), and (iv) 2016–2019 (with a total of 176 articles with a peak of 48 publications in 2017, with an average of 44 articles per year). This shows an increasing trend of studies being undertaken on mountain region plant invasions (Fig. 13.1).

There was inconsistency in the number of studies being undertaken on mountain region plant invasion across the continents. The majority of the studies were from Europe (32.3%; $n = 262$), with the highest number of studies reported from Switzerland ($n = 48$) and Germany ($n = 43$), followed by North America (27.1%; $n = 226$; with the highest number of studies conducted in the USA; $n = 201$), then

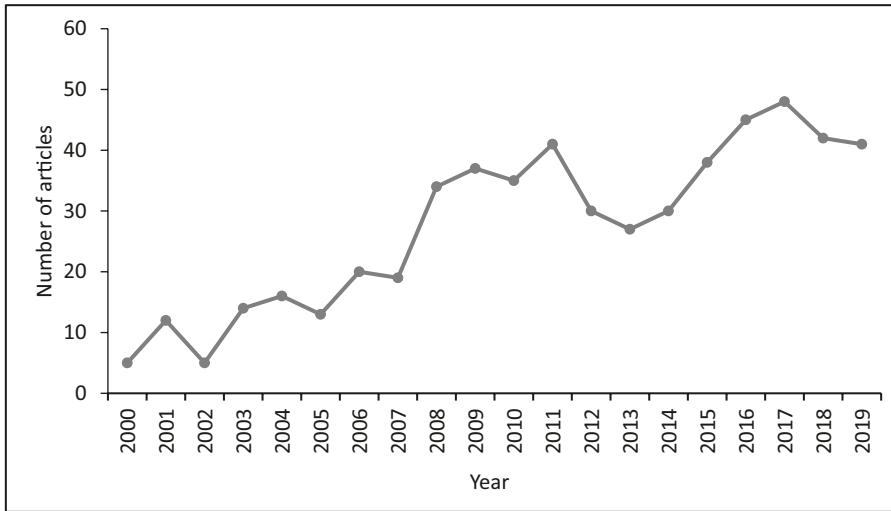


Fig. 13.1 Temporal trend of the number of plant invasion articles published over time in mountain regions

Asia (14.7%; $n = 123$; with the highest number of studies conducted in India, $n = 61$, and China, $n = 29$), finally South America (11.4%; $n = 95$; with the highest number of studies conducted in Argentina, $n = 38$, and Chile, $n = 34$). Very few studies were reported from Australia (8.5%; $n = 71$) and Africa (5.7%; $n = 48$; with the highest number of studies reporting from South Africa; $n = 41$) (Fig. 13.2).

13.3 Patterns of IAPS Richness Along Elevation Gradients

In recent years, there has been great interest in understanding the patterns and processes of biological invasion in mountain ecosystems. Owing to their steep climatic gradients, mountain regions provide an ideal environment for studying species richness and for drawing conclusions on the potential range expansion of invasive plants across latitudes. Climatic and non-climatic drivers play an important role in determining IAPS richness at a spatial scale (Vicente et al. 2013, 2019). Among the non-climatic drivers, anthropogenic disturbance is one of the most important factors in determining the pattern of invasive plant species richness along an elevation gradient (Lembrechts et al. 2016). IAPS distribution along elevation gradients in

mountainous regions has been recorded in Asia (Wang and Wang 2006; Bhattarai et al. 2014; Zhang et al. 2015; Ahmad et al. 2018; Yang et al. 2018a), Australia (McDougall et al. 2005; Bear et al. 2006; Mallen-Cooper and Pickering 2008; Beaumont et al. 2009), Europe (Becker et al. 2005; Alexander et al. 2011; Haider et al. 2011; Siniscalco et al. 2011; Kueffer et al. 2013; Dainese et al. 2014; Braun et al. 2016; Petitpierre et al. 2016; Seipel et al. 2016), North America (Pauchard et al. 2003; Daehler 2005; Bromberg et al. 2011), South America (Pauchard and Alaback 2004; Peña et al. 2008; Tecco et al. 2016), and Africa (Zenni et al. 2009; Piironen et al. 2018; Witt et al. 2018), and a global comparison has also been made (Seipel et al. 2012). However, these studies on invasive species distribution along elevation gradients have not included all the mountain regions of the world, especially the Central Asian mountains. McDougall et al. (2011a) compared alien species distribution in 13 mountain ranges around the globe. Guo et al. (2018) compared 65 case studies on the elevational distribution of native and non-native plants around the world's mountains, while many studies have considered roadside distribution patterns of invasive alien species along elevation gradients (Arévalo et al. 2005; Kosaka et al. 2010; Paiaro et al. 2011; Pollnac et al. 2012; Lembrechts et al. 2014;

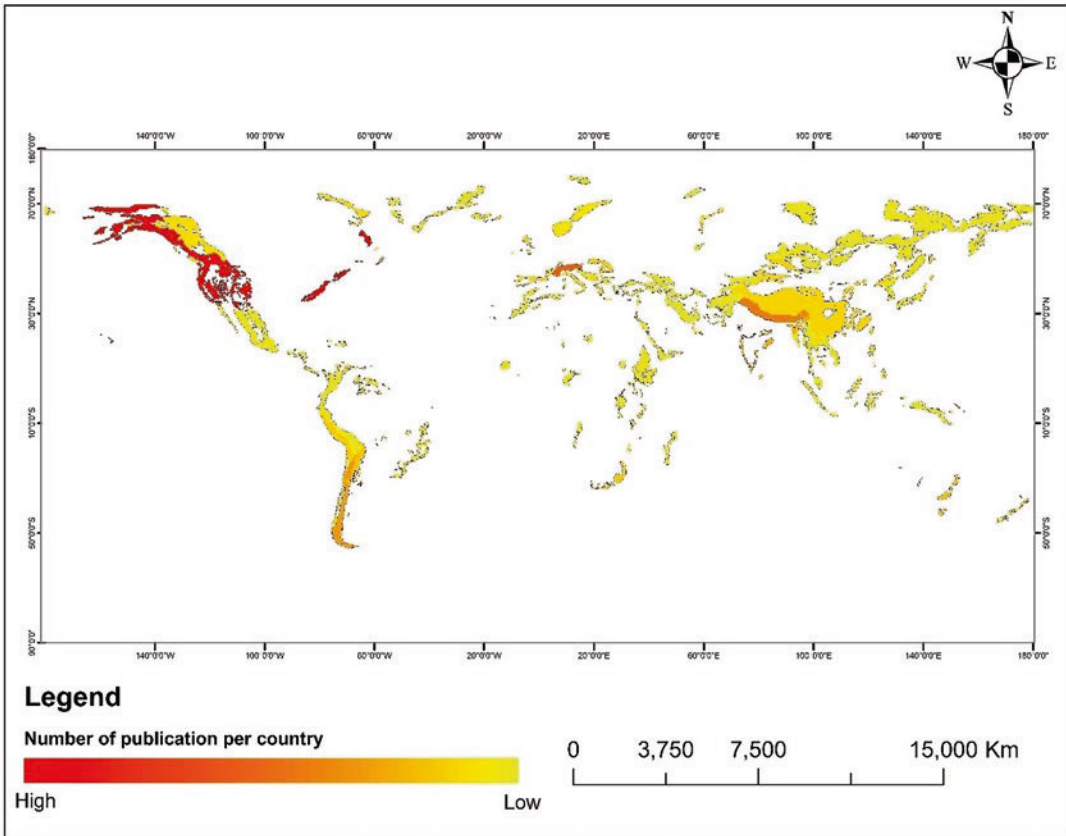


Fig. 13.2 Spatial distribution of plant invasion studies in mountain systems around the world. (Global mountain GIS data layer has been adopted from Körner et al. 2017)

Bacaro et al. 2015; McDougall et al. 2018). The majority of these studies on elevation gradients have reported that the number, abundance, and richness of alien species usually decline with increasing elevation (Pauchard and Alaback 2004; Kalwij et al. 2008; Pauchard et al. 2009; Kosaka et al. 2010; Seipel et al. 2012). This pattern is mainly caused by the range expansion of a species which first establishes at a lower elevation and then at a higher elevation, coupled with directional ecological filtering (Alexander et al. 2011). Therefore, alpine areas have not yet experienced a high level of invasion by alien plants, while the distribution of existing IAPS is usually concentrated on roadsides and in disturbed sites (Pollnac et al. 2012; Kueffer et al. 2013). In addition, many studies have shown that the invasive species are predicted to increase their distribution under future climate condi-

tions (Jaryan et al. 2013; West et al. 2015; Petitpierre et al. 2016; Carboni et al. 2018; Shrestha et al. 2018b; Srivastava et al. 2018; Thapa et al. 2018; Fernandes et al. 2019; Lamsal et al. 2019; Thiney et al. 2019).

13.4 Introduction Pathways to and Spread Within Mountain Regions

13.4.1 Human Colonization and Alien Plants in Mountain Regions

Diversity of naturalized alien species in mountain regions across the world and within their present-day native range corresponds well with the historical and current human migration and

colonization activities. The predominance of plant species native to Europe, in the alien flora of mountain regions worldwide, probably reflects the history of colonization by Europeans, particularly in the Americas and in Australia (McDougall et al. 2011a). For example, the majority of these alien plants (52%) found at elevations >2000 m asl in the Hawaiian Islands are native to the temperate regions of Europe and Eurasia (Daehler 2005). Alien plants in the mountains of Australia (Alps and Snowy Mountains) are native to Europe and Asia (Johnston and Pickering 2001). Similarly, 90% of the 128 alien plant species found in the treeless alpine regions of the Australian Alps are natives of Europe (McDougall et al. 2005). Of the total 972 alien plant species reported from 13 mountain regions of the world, many of them are native of Europe (64%) and/or Asia (45%) (McDougall et al. 2011a). The majority of the 375 alien species from 8 mountain regions representing the New World (South and North America and Australia) and the Old World (Europe) are natives of temperate Europe (150 spp., 40%), followed by the Americas (81 spp., 21.6%), Asia (17 spp., 4.5%), and Africa (16 spp., 4.3%) (Seipel et al. 2012). In other words, mountain regions in the New World have more alien plant species than mountain regions in the Old World, and this probably reflects the intentional and inadvertent introduction of species to the New World during European colonization (Seipel et al. 2012).

The majority of alien plant species found in the subtropical mountains of Asia, however, are natives of temperate Asia, Europe, and America (Khuroo et al. 2007; Yang et al. 2018a). Out of the 571 alien plant species reported from Kashmir Himalaya, 38% are native to Europe and 27% to Asia (outside of the Indian subcontinent) (Khuroo et al. 2007). Similarly, in the Laojun Mountain National Park, China, in the Eastern Himalaya, Yang et al. (2018a) reported 61 alien species, of which nearly 66% (38) were natives from America, 17 species from Europe and/or Asia, and 4 species from Africa.

13.4.2 Intentional and Inadvertent Introductions

Many of the alien plants in mountain regions have been intentionally introduced for their provisioning (e.g., food, fodder) and aesthetic values (e.g., garden plants, avenue trees) and to restore degraded habitats (McDougall et al. 2011a). In the Australian Alps, alien plants were introduced mainly for habitat rehabilitation that had been degraded due to overgrazing, e.g., hare's-foot clover (*Trifolium arvense*) and common bent (*Agrostis capillaris*) and as ornamental plants, e.g., columbine (*Aquilegia vulgaris*) and spearmint (*Mentha spicata*) in gardens (Johnston and Pickering 2001). Species introduced intentionally may easily escape and establish in the natural environment. According to McDougall et al. (2005), ornamental plants grown in the gardens of ski resorts are highly likely to escape to the natural environment and establish subsequently because they are often carefully selected for their capacity to grow at low temperatures in the mountains.

Though many alien plants have been purposely introduced in the mountain regions, others have accidentally arrived. Therefore, the pool of alien species in mountain regions consists of species introduced intentionally or inadvertently. In the montane region of the Hawaiian Islands, alien species are believed to have arrived as contaminants in seed, lots of pasture species, hay for animal feed, seeds attached to imported animals, and deliberate introduction as fodder plants (Daehler 2005). Similarly, out of 571 alien species reported from Kashmir Himalaya, 58% (332 species) were introduced intentionally for ornamental (119 spp.), food (72 spp.), fodder (50 spp.), plantation (32 spp.), landscaping (22 spp.), medicinal (20 spp.), and horticultural use (17 spp.) (Khuroo et al. 2007). The remaining 42% species (239 spp.) arrived in the Kashmir Himalaya accidentally. In the Chinese Laojun Mountain National Park in Eastern Himalaya, slightly more than half (33) of the 61 alien species were introduced inadvertently, while the

remaining species were introduced for food, fodder, medicinal, or ornamental purposes (Yang et al. 2018a).

13.4.3 Local Dispersal

Alien species generally have a short history of colonization in their introduced range and, unlike native species, are often not in equilibrium with the climatic limit of their distribution. Depending on the length of time that alien species have persisted in an area (minimum residence time, MRT), their distribution may be wide or localized (Pyšek and Jarošík 2005). The more widespread alien species often have a longer introduction history (and thus a longer MRT) than those alien species which are localized in their distribution (Shrestha 2016). However, localized distribution of alien species could be due to multiple factors, such as species traits (e.g., slow growth, low reproductive output), habitat/climatic suitability (e.g., unsuitable habitat and stressful climatic conditions), and short introduction history (e.g., recent introduction). The spread of some alien species from lowland to high elevation in the mountains is constrained by abiotic stress (e.g., low growing season temperature) and unsuitable life form (e.g., annual herbaceous life form being less successful in high-elevation environment) instead of dispersal limitations (Alexander et al. 2011; Rundel and Keeley 2016).

Since mountain invasions are mostly a relatively recent phenomenon, many of the alien species are still in the early stages of invasion, and they may not have reached their ecological niche boundaries. In other words, the current upper elevation range of distribution of many alien species might be well below the full range as determined by climatic constraints. When such species are dispersed to the higher elevation, their establishment will not be constrained by climatic factors. For example, when seeds of three woody alien species (*Pyracantha angustifolia*, *Ligustrum lucidum*, and *Gleditsia triacanthos*) were sown at elevations higher than their current distribution in the mountains of central Argentina, seeds germi-

nated and the seedlings successfully overwintered, suggesting the absence of climatic constraints for these species at these higher elevations (Tecco et al. 2006). However, the heterogeneous nature of the mountain landscape does not allow for the rapid spread of most alien species due to the absence of a continuous suitable habitat within the region with a suitable climate. In such situations, the rate of spread of an alien species and their range size depends on the availability of dispersal corridors. In the mountain landscape, human-made infrastructure, as well as natural corridors, has served as dispersal pathways for alien species. Road construction in mountain areas not only opens new dispersal corridors for alien species but also increases the area of land that is disturbed where the probability of establishment of alien species is high. Infrastructure developments related to tourism (e.g., resorts) and recreational activities (e.g., skiing) have also increased the areas under intense disturbance in the mountain regions. Since infrastructure development and recreational activities are projected to increase in the future, the disturbed areas suitable for the establishment of alien species are expected to increase further in the future. Most of the studies so far, examining distribution and dispersal of alien plants in mountainous regions around the world, have used road and/or hiking trails as their reference (e.g., Johnston and Pickering 2001; Johnston and Johnston 2004; Seipel et al. 2012; Yang et al. 2018b; Liedtke et al. 2020), suggesting that road networks are predominantly the important dispersal pathways for alien species in these regions. These studies have also reported higher numbers of alien species and their abundance along road verges relative to adjacent natural habitats (Johnston and Johnston 2004; Kalwij et al. 2008; Pollnac et al. 2012; Seipel et al. 2012; Dar et al. 2015). In a survey along roads and trekking trails in Laojun Mountain National Park of China in Eastern Himalaya, Yang et al. (2018a) reported that all the alien species found at higher elevations were also found at lower elevations and have been able to pass the climatic filter, suggesting that the lowland alien species pool serves as the source of propagules for plant invasions in the

higher elevations (Alexander et al. 2011). Besides road networks, the alien species are also known to use natural dispersal pathways such as watercourses. For example, Lu and Ma (2006) reported streams to be a major natural dispersal corridor for Crofton weed (*Ageratina adenophora*) in southwestern China. Similarly, in the Sierran Steppe ecoregion of the mountains in northwestern continental USA, many alien species are found to be common along the natural dispersal pathways that include streams and rivers (Parks et al. 2005). In addition to suitable dispersal corridors, the spread of alien species in the mountainous areas also depends on the degree of habitat disturbance. As in lowlands, alien plants in mountain areas also prefer disturbed habitats. For example, in the Australian Alps, disturbed areas mainly associated with the construction and operation of tourist facilities have been shown to have high numbers of alien plants (Johnston and Pickering 2001).

Microclimatic variation that is prevalent in mountain regions may also provide an opportunity for some alien species that have efficient dispersal modes. Even when the general climatic conditions above the current elevational limits of alien species are unsuitable for them, there may be suitable microclimatic conditions that can serve as a stepping stone for further spread to higher elevations through the establishment of satellite populations (Lembrechts et al. 2017).

13.5 Drivers of Plant Invasions into Mountainous Areas

Pauchard et al. (2009) identified four major factors that govern plant invasions in the mountainous areas, which include (1) preadaptation of alien plants to the abiotic mountain environment, (2) low biotic resistance due to low diversity of species and biomass of native communities and the increasing importance of facilitation (establishment of alien species being facilitated by natives) at high elevation, (3) anthropogenic disturbances leading to the creation of suitable habitats for alien species, and (4) increasing propagule pressure due to improved access to previously

less accessible mountain areas and increasing introduction efforts in tourist facilities including ski resort gardens. The important roles of these factors in driving the process of plant invasions in mountain regions are discussed below.

13.5.1 Plant Traits

Plant traits such as life form, adaptation to low temperature, and breadth of ecological amplitudes determine the success of alien species in the mountainous areas. In high-elevation mountain regions such as treeless alpine areas, perennial herbs are the most successful among the native species. Therefore, it is highly likely that perennial herbaceous alien species may also establish well in high mountain regions if they can cross the environmental filter of low-temperature tolerance. In line with this prediction, McDougall et al. (2011a, 2018) have shown that the alien flora of mountain regions worldwide is mostly herbaceous but with nearly equal proportions of annual and perennial species. The preadaptation of alien plant species to low temperature increases the probability of their successful establishment and spread in mountain regions. This is to be expected when alien plants of one mountain region are native to another mountain region or high-latitude regions. This probably explains why many of the alien plants (52%) found above 2000 m asl in the Hawaiian Islands are the natives of temperate regions of Europe/Eurasia (Daehler 2005). Similarly, McDougall et al. (2018) showed that invasion by alien species from road verges to adjacent natural habitats depends on the traits of the alien species. For example, among alien species growing along the road verges in the mountains of Argentina, Australia, Chile, Norway, and the USA (Montana and Oregon), only those species which were tolerant to shade, and high moisture, spread into the adjacent natural habitats (McDougall et al. 2018).

Invasive alien species are generally characterized by wide ecological breadth with their capacity to thrive in a wide range of environmental conditions. This appears to be true for the alien species of the mountain regions as well.

Generally, the alien species of the mountains worldwide have a wide distribution from lowland to highland in their native range instead of being highland specialists (McDougall et al. 2011a). Therefore, it is expected that alien plants first establish in lowland areas due to the proximity of the propagule sources, and subsequently, these alien species spread to mountain regions using natural or human-made dispersal corridors. This expectation has been supported by empirical data, which shows that in the Laojun Mountain National Park of China in Eastern Himalaya, all the alien species found in the higher elevations were also found in the low elevations (Yang et al. 2018a).

13.5.2 Native Plant Diversity and Facilitation

The diversity of native vascular plants in mountain regions generally shows a unimodal response to elevation with repetitive decline above the region with their highest diversity (Averett et al. 2016). Therefore, high mountain regions are relatively poor in plant diversity, and such species-poor communities are considered to have low biotic resistance against invading alien species (Zefferman et al. 2015). However, at the microhabitat (plot) level in the Australian Alps, the richness of alien plants increased with the increasing richness of native plants (McDougall et al. 2005).

Another community trait that may promote invasion in high mountain areas is the increasing importance of facilitation in shaping species composition (Tecco et al. 2016). It seems paradoxical to note that some of the alien plants exploit suitable microhabitat created by native cushion plants in the alpine region, which is otherwise unsuitable for alien plants. For example, in the Chilean Andes, the growth and abundance of the alien dandelion (*Taraxacum officinale*) is higher within the microhabitat created by a native plant (*Azorella monantha*) than in the habitat away from the cushion (Cavieres et al. 2005). Within the cushion of the native plant, the alien *T. officinale* had higher seedling survival, net photo-

synthetic rate, and stomatal conductance than in the habitat outside the cushion.

13.5.3 Disturbances

Since invasive species are mostly ruderal, spatio-temporal variation in disturbance is an important contributing factor to the diversity and distribution of alien invasive species in mountainous areas. In the tropical mountains of Ecuador (Andes), alien species are dominant in disturbed areas associated with road construction and maintenance (Sandoya et al. 2017). Averett et al. (2016) reported that alien species are mostly confined to the disturbed and open canopy habitats in the Wallowa Mountain Range of northeastern Oregon (USA). An increase in cover, as well as the number of alien species, has been reported after a fire in the Australian Alps (McDougall et al. 2005). Similarly, in the mountains of northwestern continental USA, land disturbance plays an overwhelmingly important role in the establishment and spread of alien species (Parks et al. 2005). In these mountain regions, the alien species are largely confined to the early successional communities that develop after disturbance while becoming rare as the vegetation changes to late-successional communities such as old-growth forests (Parks et al. 2005).

13.5.4 Propagule Pressure

Improved access through expanding road networks to previously less accessible mountain areas and the increasing introduction efforts of alien species without any regulation in tourist facilities such as ski resort gardens have increased the propagule pressure of alien species in these regions (McDougall et al. 2005). Road construction not only increases the propagule production of alien species but also increases suitable areas (i.e., disturbed) for their establishment. Where there is a road, alien species establish first along the verges, and then some may spread into the adjacent natural habitats (McDougall et al. 2018). The number of hotels and resorts including ski

facilities for tourists has been increasing in mountain regions (Moreno-Gené et al. 2018). Transportation of construction materials to develop such facilities also increases the probability of alien species hitch-hiking to the site, while disturbance increases the area surrounding the construction sites for their establishment (Rew et al. 2018).

13.5.5 Climate Change

Invasion risks in mountain ecosystems will increase greatly over time, as climate change continues (Barni et al. 2012; Petitpierre et al. 2016; Shrestha et al. 2019). Because of their steep environmental and climatic gradients, mountains are recognized as being especially sensitive to climate change (Beniston 2003). Climatic change, involving increased atmospheric temperature, altered precipitation, and elevated atmospheric carbon dioxide concentrations are all likely to enhance invasion (Yan et al. 2017) by creating new climatically suitable areas for invasive species to enter, especially at the higher altitudes. Increased temperature is likely to either cause a range expansion of invasive species from lower elevations, including the pre-adapted invasive species (Bradley et al. 2009, 2010; Petitpierre et al. 2016), toward the higher elevations (Alexander et al. 2011; Marini et al. 2013). Reduction in snow cover due to increased temperature is also likely to increase the chances of invasion (McDougall et al. 2005).

Mountains generally have a smaller number of alien species than their surrounding lowlands because the prevailing low temperatures in mountains prevent the upward movement of many alien species. However, the risk of plant invasions at higher elevations in mountain regions is likely to increase in the future as climate change continues. Species distribution modelings have consistently predicted the upward shift of the upper elevation limits of alien species currently present in the mountain landscape (Petitpierre et al. 2016; Carboni et al. 2018; Lamsal et al.

2018; Shrestha et al. 2018b; Shrestha and Shrestha 2019). In situations where the upper elevation limit of alien species distribution is already close to their niche boundaries, rapid spread to high elevation is less likely to occur in the near future (Seipel et al. 2016). This situation arises when the alien species were introduced into a region long before their distribution had reached an equilibrium with the current climate. However, climate change in the future may elevate the niche boundaries of species to higher elevations and facilitate the spread of such alien species to higher elevations (Seipel et al. 2016). Thus, it is very important to identify the climatically suitable areas into which an invasive species can move and quantify risks associated with this. There will also be opportunities in the future climate scenarios for land managers to prevent and appropriately manage invasive species expansion in the mountains (Bradley et al. 2009; McDougall et al. 2011a; Shrestha et al. 2018b). Despite this, a greater understanding of invasion risk under climate change is crucial in developing effective policies and programs to manage invasive species and reduce their impact on biodiversity and ecosystem function (Bradley et al. 2010).

13.6 Impacts of Invasive Alien Plant Species

Invasive species are an important component of global environmental change. Invasive alien species disrupt ecosystems (Dogra et al. 2010; Vilà et al. 2011), compete with native species (Brown et al. 2002; Muñoz and Cavieres 2008; Dutra et al. 2011), and cause economic losses (Zavaleta 2000; Gerlach 2004; Eagle et al. 2007). The impact on species diversity and composition of invaded communities differs between individual invaders. Almost 1000 plant taxa have been reported to be naturalized or invasive in the 13 mountain regions of the world (McDougall et al. 2011a). These species often have tolerance to cold environments and might pose an important threat to biodiversity (Lembrechts et al. 2016).

13.6.1 Impacts on Environment and Biodiversity

The establishment of invasive plants poses a serious threat to biodiversity and ecosystem functioning in the mountains (Allsopp and Holmes 2001). Invasive plants deliberately or accidentally introduced into mountain ecosystems have resulted in reduced species richness, abundance, diversity (Cavieres et al. 2005; Reinhart et al. 2005; Reshi et al. 2008; Khuroo et al. 2010; Lembrechts et al. 2017; Haider et al. 2018), and decreased biomass and productivity of native plants (Mallen-Cooper and Pickering 2008; Molina-Montenegro et al. 2012). The invaded community, thus, experiences species homogenization and a denser canopy cover particularly due to the rapid spread of invasive trees and shrubs (Reinhart et al. 2005; Khuroo et al. 2010; Ayup et al. 2014). Some invasive plants have caused a dramatic change in plant community composition and reduce local species diversity by suppressing the natural regeneration and growth of most native plants and enhancing the growth of other exotic species (Wearne and Morgan 2004; Reinhart et al. 2005; Pritekel et al. 2006; Tecco et al. 2006; Khuroo et al. 2010). In the northern foothills of the Tatra Mountains, Himalayan balsam (*Impatiens glandulifera*) was found to suppress weak competitors and impact plant diversity negatively (Kiełtyk and Delimat 2019). Plant invasion in the mountain ecosystems thus alters the species composition over time and increases invasion pressure (Wolf et al. 2003; Tecco et al. 2006).

The impacts of invasive species on native biodiversity can be further influenced by the resultant changes in soil properties with reduced moisture content, organic matter, and altered nitrogen concentration and minerals (Wolf et al. 2004; Pritekel et al. 2006; Zeidler et al. 2012). It has been found that in the Rocky Mountain National Park, USA, invasion by Canada thistle (*Cirsium arvense*) and leafy spurge (*Euphorbia esula*) changed soil properties and impacted the soil fauna density and their functioning (Pritekel et al. 2006). Invasive alien species in mountain areas are reported to cause a significant decline in

alpine beetle species (Kašák et al. 2015). Furthermore, invasive species interfere with the interaction between the native plants and their pollinators. In high-elevation alpine environments, invasive plants have threatened native pollination services and have caused a negative impact on native bee populations (Miller et al. 2018). Additionally, invasive plants are also known to impact the avifauna diversity of mountainous areas resulting in lower species richness, diversity, and abundance (Ayup et al. 2014). For example, coastal wattle (*Acacia cyclops*) invasions have adversely affected the birds of Mountain Fynbos in South Africa (Fraser and Crowe 1990). Modeling studies have also shown that invasion dynamics in the Himalayan region may have future potential impacts on multiple ecosystems and their biota (Lamsal et al. 2018; Thapa et al. 2018).

13.6.2 Impact on Ecosystem Services

Invasive alien plant species often negatively affect various ecosystem services (Vilà and Hulme 2017; Keller et al. 2018). Invasive species can both positively and negatively impact agricultural production and can reduce crop yields (Rawat et al. 2019). In California rangelands, the growth of an unpalatable invasive species yellow starthistle (*Centaurea solstitialis*) has been found to reduce forage availability and quality, thus causing the decline of livestock production and resulting in significant economic losses (Eagle et al. 2007). Likewise, invasive species may also have negative impacts on water regulation (Le Maitre et al. 1996). For example, in South Africa, increased invasions have caused a significant impact on streamflows throughout the Western Cape Water Supply System (Le Maitre et al. 2019), threatening the catchment areas with erosion, and have degraded the water quality in catchment areas (Enright 2000). In Table Mountain National Park, South Africa, pine invasion in the fynbos biome has provided ecosystem services such as carbon sequestration and fuelwood but has also caused a significant negative impact on water runoff, thereby reducing

biodiversity (van Wilgen 2012). In addition to mountains being treasured landscapes for tourism and recreation, invasive species can reduce the value of the recreational area in these regions. For example, Lake Tana, which is the largest lake in the highlands of Ethiopia, has been invaded by water hyacinth (*Eichhornia crassipes*), and dense mats of the species blocked waterways, inhibiting boat traffic, fishing, and recreational activities (Dersseh et al. 2010; Abera 2018).

13.6.3 Socioeconomic Impacts

The impacts from invasion by alien plants on the ecosystem services sometimes result in a huge economic loss (Zavaleta 2000; Gerlach 2004; Eagle et al. 2007) and cause serious impacts on the livelihood of mountain communities, particularly in crop and livestock production. For example, invasions caused a reduction in pasture availability for livestock and have resulted in huge economic losses to the herders, thus putting local livelihoods at risk in those regions (Khuroo et al. 2010). Invasive species were found to reduce crop production, increase labor input in weeding, and reduce forage production in the Chitwan Annapurna Landscape of Nepal (Shrestha et al. 2018a). In the Mulanje Mountain Forest Reserve, Malawi, invasive species have caused a negative impact on food security and infrastructure, damaged firewood and medicinal trees, and reduced water supply and tourism (Shah and Makhambera 2019). Similarly, parthenium weed (*Parthenium hysterophorus*), which is expanding rapidly in the Himalayan Mountains, has caused negative impacts on forage supply as well as the health of livestock and human beings (Kohli et al. 2004, 2006; Shrestha et al. 2018b). There is still a lack of information on the impacts of IAPS on rural mountain communities. However, there is a need for more research on the socioeconomic impacts of IAPS on the livelihoods in the mountains. The information can be used as evidence to promote the control and management of IAPS. Although invasive plant species are reported to cause

harmful impacts on biodiversity and ecosystems, there are instances of positive impacts on the livelihood of mountain communities, particularly for rural low-income communities. For example, mountain communities acquire benefits from invasive plant species through the provision of ecological goods and services such as timber, medicine, charcoal, and fuelwood (Turpie et al. 2003; De Neergaard et al. 2005). Lantana (*Lantana camara*), one of the world's 100 most invasive species, is infesting millions of hectares of land, causing huge socioecological impacts, and management of this species has remained a major challenge in Africa, Asia, and Australia (Bhagwat et al. 2012). At the same time, *L. camara* has served to support livelihoods in several mountain communities in India, as local communities use it for fuelwood, furniture, and pulp-making (Negi et al. 2019; Pathak et al. 2019).

13.7 Management

13.7.1 Management Approaches

Prevention

Mountains are probably one of the only places where preventive management actions could work efficiently (Leung et al. 2002; McDougall et al. 2011a). Preventive measures include (1) identification and control of potential invasive plants that may be introduced from the lowlands; (2) studying future environmental challenges, such as climate change, horticulture, and tourism developments; (3) understanding and targeting major introduction pathways; (4) prioritizing the prevention of species that are already of concern in other mountain areas; (5) providing training to concerned staff; and (6) educating visitors and local people about the negative consequences of biological invasions (McDougall et al. 2011b). Another effective prevention measure is risk assessment of alien ornamental species and removal of those that have a high potential to be invasive in mountain regions (McDougall et al. 2011a).

Early Detection and Eradication

Early detection and response with surveillance and the removal of plants found in mountain areas have been reported to be the most effective strategy for the management of invasive plant species (Kueffer et al. 2014). Early detection and rapid response is the most commonly used surveillance method and uses knowledge concerning seed dispersal mechanisms to maximize the chances of finding and destroying new incursions (Fox et al. 2009). Habitat that is susceptible to invasion, identified based on dispersal mechanisms and maximum distances, is targeted for management using the early detection and rapid response method (Fox et al. 2009). Such a strategy can be ineffective when the invasion has progressed to a level where eradication is no longer feasible (Fox et al. 2009). Thus, the feasibility and effectiveness of eradication in any new area should be determined before being attempted. For this, the spatial extent should be determined by intensively surveying the proximity of the invaded site followed by the determination of any subsequent spread (Fox et al. 2009). For example, Giljohann et al. (2011) used a spatial model to optimize search and control efforts for invasive common sallow (*Salix cinerea*) in the Australian Alps.

Cultural, Physical, and Mechanical Control

Some mechanical control approaches, such as mowing, slashing, cutting, and burning, were often used in reducing the abundance of certain non-native plants and increasing the abundance of natives, with an overall increase in species diversity (Price and Weltzin 2003; McDougall et al. 2011b; Shrestha 2019). In addition, some mountainous areas have also implemented prescribed grazing and weed-free programs to help prevent invasions (McDougall et al. 2011b). Local utilization and manual uprooting are cultural methods practiced in invasion management that help in reducing cost and enhancing the benefits of invasive plants (Kannan et al. 2016; Shrestha 2019). Some invasive plants such as water hyacinth are reported to be used for food production, water purification, and energy pro-

duction through biogas and briquette preparation (Kafle et al. 2009). Promoting utilization of invasive plants, which have significance to local livelihoods, may be a feasible approach in controlling their spread and preventing their negative consequences for native biodiversity (Kannan et al. 2016). Considering the social aspects of invasive species management, control programs should also take into account the active participation of local people, their level of knowledge, and species selection (Shrestha 2019; Shrestha et al. 2019).

Furthermore, fire can be used to manage the expansion of invasive species, especially woody tree species, helping to increase the disturbance return interval (average time before fire re-burns a given area) and, thus, decrease the competitive advantage, abundance, and impact of invasive species on the ecosystem (Ansley and Rasmussen 2005; Fairfax et al. 2009). The use of fire should be integrated with pre-fire felling and burning after 1–2 years for plants with winged seeds and follow-up weeding for improved efficiency (van Wilgen et al. 2016). Mechanical removal of woody invasive species has been described as an effective tool in the management of invasive species in Africa (Van Wilgen et al. 1997). Likewise, site-specific extirpation was reported as a feasible management option for the invasive hillock bush (*Melaleuca hypericifolia*) in South Africa (Hickley et al. 2017).

Biological Control

Some invasive plants can also be controlled by biological control agents in the mountains (Moran and Hoffmann 2012). Insects and fungi have the potential to act as biological control agents of some alien plants by weakening the growth of these plants (Wu et al. 2014). However, to be successful, biological control programs should focus on the characteristics of the biological control agent, its potential distribution, and abundance in the release site (Wu et al. 2014). Developing biological control methods could be an effective way of controlling aggressive invasive plants (van Wilgen et al. 2016). Conversely, it was noted that mountainous countries allocate only a small part of their total invasion control

fund for the use of biological control (Van Wilgen et al. 1997).

Ecosystem-Based Management

Manual labor, handsaws, and axes should be replaced with chainsaws and brush cutters and follow-up operations for more efficient eradication of unwanted plants (van Wilgen et al. 2016). Management strategies for plant invasions in the agricultural sector of mountainous areas should focus on early detection and rapid response (McDougall et al. 2011b). Other management activities in mountain areas like Kashmir Himalayas and Australia have been directed toward costly eradication programs for invasive plant control in horticulture, agriculture, and freshwater lakes (McDougall et al. 2011b). In Cades Cove, Great Smoky Mountains National Park, USA, ecological restoration has been found to reduce the spread of invasive species (Price and Weltzin 2003).

Support Tools for Management

Decisions

Species distribution models (SDMs) are scientifically proven tools (Guisan et al. 2013) that can provide timely information concerning the area at risk of being invaded and to the decision-makers helping them to devise effective control and management strategies for invasive species in mountain areas. A recent study has demonstrated the significance of using SDMs, mainly to predict invasions of the silver wattle (*Acacia dealbata*) in mountainous protected areas of Portugal and Spain (Fernandes et al. 2019) and to identify invasion hotspots in high-elevation mountainous regions of Nepal (Shrestha and Shrestha 2019).

13.7.2 Challenges and Opportunities

The major management challenges in mountain regions are to limit the upward movement of invasive plant species, to protect native species (Pauchard et al. 2009, 2016), and to link various processes operating at the local and larger scales (Kueffer et al. 2013). Furthermore, management

methods can be difficult to implement when there is uncertainty of associated risk factors in the future (McDougall et al. 2011b). Thus, before the implementation of any costly control programs, an economic analysis of the costs and benefits of the management program must be done (Van Wilgen et al. 1997). Decisions should be made based on the knowledge of invasive plants and the environment, and implementations should be cost-effective (McDougall et al. 2011a).

The control of invasive species is important if the proper regulation and flow of ecosystem services, such as natural resource management, water supply, water flow regulation, and livelihood support, are to be maintained (Cavaleri et al. 2014). Some intensive invasion management programs also provides employment opportunities, enhanced stewardship, and training to locals and women empowerment through water and natural resource security and consequently increases community governance among locals (Everard et al. 2018). Thus, control and management of invasive species may provide benefits in terms of tourism, local employment, and fodder provision (McDougall et al. 2011b). Invasive plants are also used as medicine, compost, charcoal, briquette, and energy feedstock and for controlling floods and landslides by the local people (Kafle et al. 2009; Spinelli et al. 2016; Shrestha 2019; Shrestha et al. 2019). Invasive species in some mountainous areas have been providing local people with beneficial provisioning and regulating services. For example, Siam weed (*Chromolaena odorata*), Lantana, and Crofton weed are reported to be used as sources of biomass for compost, charcoal, and bio-briquette; Billy-goat weed (*Ageratum conyzoides*), cobbler's pegs (*Bidens pilosa*), hairy galinsoga (*Galinsoga quadriradiata*), and touch-me-not (*Mimosa pudica*) are used as forage for livestock; leaf paste of Siam weed, Crofton weed, and Billy-goat weed are used to treat cuts and wounds; the root of spiny amaranth (*Amaranthus spinosus*) is used to treat urinary tract obstruction and tender plants of this species are consumed as a vegetable by the people in the mountainous areas of Nepal (Shrestha et al. 2019).

Along with local uses, invasive plants are also reported to provide other ecosystem services, such as control of floods by pink morning glory (*Ipomoea carnea* ssp. *fistulosa*), and stabilization of landslides by Crofton weed and pink morning glory (Shrestha et al. 2019). Local communities living near the Table Mountain National Park in South Africa planted alien woody species, such as *Pinus* species and *Eucalyptus* species, for recreation, but these tree species have adverse impacts on hydrology, fire intensity, and soil stability (van Wilgen 2012). Therefore, it should be further noted that the negative impacts of particular invasive species might far outweigh their benefit, and any use of invasive species should be identified as a part of integrated management. The use of invasive species should not promote further spread of the species as this may increase the probability of people introducing species into new areas for their beneficial uses while underestimating their future devastating impacts.

Invasive species management will be an expensive and challenging task once the species spread into a topographically complex mountain ecosystem. Therefore, sharing information from different mountain regions through the formation of networks at local to global levels is important for raising awareness and devising effective management strategies against invasive species (Kueffer et al. 2013). Management requires a sound understanding of the patterns and drivers of plant invasions. MIREN is working toward these objectives and the extension of these approaches to all mountain systems. The main goal of the network is to understand the effects of global change on species distributions and biodiversity in mountainous areas by performing observational and experimental studies along elevation gradients. MIREN currently incorporates over 20 mountain regions that participate in standardized baseline screening and monitoring, while simultaneously looking for data providers or collaborators particularly from underrepresented mountain regions, which may help to get information in making better management decisions (Dietz et al. 2006). The MIREN network provides opportunities to better understand invasive species dynamics in mountain areas, which

is essential for the long-term management of invasive species in the mountains.

13.7.3 Lessons for Better Management Strategies

Invasive species management in mountain areas is unique, and thus management strategies should be appropriately designed to this unique setting. Before applying any management practices, specific responses should be studied and quantified in the targeted ecosystems (Ansley and Rasmussen 2005). First, invasion management plans developed for mountainous areas should include preventive measures. In particular, there is a need to understand major introduction pathways for enhancing prevention. To accomplish this, mountain managers need to do cost and benefit analyses, ensure public acceptance, identify the impact of climate change on invasion, and, finally, demonstrate better management outcomes through prevention (McDougall et al. 2011b). Second, cooperation among and active participation of local communities, governmental agencies, and non-governmental organizations are essential for efficient and long-term management of invasive alien species (Zhang et al. 2019). Third, allocation of resources and prioritization of target species are other prerequisites for effective invasion management (Shrestha et al. 2019). Finally, as biological invasions are a common problem in many world regions, common planning and control through cooperation are highly effective for the prevention and control of invasions (Rashid et al. 2009; Fuentes et al. 2010).

Management of IAPS is challenging especially in the mountains due to intrinsically rough topography. Therefore, investing funds in management without monitoring is not sufficient. Improved management needs to involve the practicing of conservation triage through decisions on which species to save from extinction and which species are too costly to save given the management efforts required via invasion management (Byrne 2016). Conservation triage includes management measures focusing only on priority areas and species (sparsely invaded areas and upper

reaches of drainage lines), accepting trade-offs between reducing invasion and biodiversity conservation and using best practice methods (fire and species prioritization) (van Wilgen et al. 2016). Integrated management approaches should be promoted involving inventory, planning, prioritization, control, monitoring and research, containment, prevention, outreach and education, and partnership and cooperation with stakeholders (Kueffer et al. 2013).

13.8 Conclusions

Although some mountain regions, such as the European Alps and Himalayas, are already being threatened by IAPS, most of the mountain ecosystems around the world are still relatively less affected by invasive plants compared to their neighboring lowland ecosystems. Anthropogenic disturbance to habitats, increased propagule pressure, and recent climate change are some of the major driving forces influencing plant invasions in these regions. It is expected that there will be an increased risk of invasion and greater management challenges in the near future. Therefore, to avoid further spread of IAPS in mountain regions, frequent monitoring and better management strategies need to be developed. In-depth research is needed to address plant invasions into mountain ecosystems, including the analysis of multi-scale invasion patterns in mountain regions, and comparative research across hemispheres on how invasive species interact in mountain environments. Future research should focus on understanding the complex interactions between anthropogenic and climate change-driven species distribution changes. In addition, comparative research across mountain regions, such as field-based experimental studies and impact assessment of invasive species, might provide valuable opportunities to understand how invasive species will respond to new environmental conditions. More importantly, development of global awareness among major stakeholders through a coordinated approach is needed to achieve effective integrated management of invasive plants in the world's mountain regions.

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Biotic and Economic Impacts of Plant Invasions

14

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Abstract

The invasion of alien species manipulates the structure, function, and composition of the recipient ecosystem causing ecological, economic, and social impacts. However, these impacts can be positive or negative, depending on the effect and context of the invasion. In some cases, invasions enhance primary productivity of the ecosystem and increase species richness. On the other hand, in the majority of cases, the invasive species displace native species, adversely impacting native ecosystem and jeopardizing natural resources. The outcome of the impacts is based on several factors, such as mode of introduction, type of invasive species, condition of the invaded habitat, and characteristics of native species. For instance, specialist native species

are predicted to suffer adverse effects, while generalists may flourish even when invasive species are abundant. There has been considerable debate in recent times about whether claims of severe impacts of invasive species are exaggerated and whether efforts to manage them are unnecessary or even harmful, and some unintended consequences of invasive species management have been documented. Regardless of the lack of consensus on the impacts of invasive species, they are posing a measurable cost to society. Invasive species severely affect agriculture, fisheries, tourism, forestry, and property values. Countries that rely on agriculture with small landholders are the most vulnerable to the invasion of exotic species. The rate of spread of invasive species is currently surging due to increased travel, trade, and transport in combination with climate change. Accurate and comprehensive information on economic and environmental impacts of invasive species is seriously lacking, and more research is needed to develop management strategies based on the impacts of invasive species.

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14.1 Introduction

Invasion of invasive alien species has occurred in almost all ecosystems throughout the world. The introduction of invasive species generally displaces the existing species in the recipient ecosystem (Huxel 1999). This may eventually lead to homogenization of the invaded habitat. There is a general consensus that an invasion of exotic species reduces plant species richness and composition. However, these impacts vary greatly among individual invaders (Hulme and Bremner 2006; Hejda and Pyšek 2008; Hejda et al. 2009). Ecosystem functions and stability rely on species richness, species composition, evenness, and genetic diversity (Isbell 2010). A change in ecosystem functions distorts the production and supply of the quality and quantity of ecosystem services, i.e., the benefits to human society provided by natural ecosystems (De Groot et al. 2002). As a result, particular groups within society may benefit from this change, whereas others will not (Rai and Scarborough 2015a).

Ecosystem services are often viewed as the interest on the ecosystem, and the ecosystem itself is considered to be the capital. Ecosystem services contribute to maintain or improve human welfare. These services have a dual contribution to the economy: as material inputs and as a sink for wastes generated during the production process (Daily 1997). This suggests that fluctuation in the supply of ecosystem services may have socioeconomic, cultural, and human health impacts. Furthermore, invasion of exotic plants may have adverse impacts on animal health (Andersen et al. 2004; Siwakoti 2007; Allan et al. 2018).

Milanović et al. (2020) were able to link traits of invasive plants with both ecosystem services and “ecosystem disservices” and developed a framework to look at how invasive plants positively and/or negatively impact six key socioeconomic and environmental sectors: agriculture, forestry, infrastructure, human health, aesthetics/recreation, and the environment. Ecosystem disservices are the harmful effects of ecosystem functions to human well-being (von Döhren and Haase 2015). For example, plant invasion may

affect livelihoods in rural communities. Compromised ecosystem services can reduce farm household productivity. Pratt et al. (2017) documented impacts of parthenium weed (*Parthenium hysterophorus*) and other invasive species on African smallholder livelihoods, finding future annual economic losses to maize production ranging from \$139.4 to 195.3 million US\$ over the four African countries studied (Ethiopia, Kenya, Tanzania, and Uganda). However, literatures on the impacts of invasive plants on economy and livelihoods are scant and inconclusive because livelihood impacts of invasive plants are based on the nature and mode of introduction of invasive plants and how household income is generated (Foster and Sandberg 2004; Laxen 2007; Shackleton et al. 2007, 2011; Rai et al. 2012; Rai and Scarborough 2015a). Even the economic effects of an individual invasive species on livelihoods may vary on a temporal scale (Shackleton et al. 2007; Rai and Rai 2013).

There is a virtual consensus that these species have adverse impacts on agriculture, fisheries, and livestock. Estimated costs attributed to invasive species vary widely due to geography, type of invasive species, and the size of economy. It ranges from one million US\$ to 12% of the gross domestic product (Marbuah et al. 2014). In the United States alone, the annual damage of invasive species is about US\$120 billion (Pimentel et al. 2008). Usually, the largest agricultural producers experience the greatest cost of invasion, but agriculture-based developing countries are generally the most vulnerable to invasive species (Paini et al. 2016). The impacts of invasive species are not straightforward, and strategies for managing invasive species need to account for the wide variation in impacts of invasive plant species. Therefore, there is an urgent need to understand the impacts of invasive plants more fully. There is a considerable amount of literature on the impacts of invasive plant species, but a disproportionate number of studies are focused on developed economies (Fine 2002). These studies have failed to capture the variation in the impacts of invasive plants as they rely on attributes of the recipient ecosystems and of the invaders and at

global scale (Levine et al. 2003; Vilà et al. 2011). This information gap limits our understanding of the true impacts of invasive plants and the ability to predict their performance in different ecosystems.

Invasive species management usually includes three successive steps: prevention, eradication, and control. The preferred strategy is to prevent the introduction of invasive species (Leung et al. 2002; Allendorf and Lundquist 2003). This is because, once the invasive species are established, eradicating or controlling them can be very challenging and expensive (Mwangi and Swallow 2008; Rai and Scarborough 2013, 2015a). Prevention also ensures that native ecosystems are undisturbed by invasive plants. For developing countries, the cost of invasion comprises a substantial proportion of their gross domestic product (Paini et al. 2016).

It is also equally true that there might be an economic motive to introduce fast-growing exotic plant species to improve agricultural production (Hallett et al. 2011) or develop new crops, e.g., for biofuels (Barney 2014). In such cases, preventing the introduction of all exotic species may be controversial. Reliable information on invasive plants may help managers to identify which species should be prohibited and which should require close observation once they are introduced. In some countries, risks are evaluated through careful screening and/or experimental trials, but the standards for assessing risk vary widely among different countries.

There are a variety of databases on invasive species that help to assess impacts. These include the Global Invasive Species Database (<http://www.iucngisd.org/gisd/>), the Invasive Species Compendium (<https://www.cabi.org/isc/>), Images of Invasive and Exotic Species (<https://www.invasive.org/images.cfm>), Delivering Alien Invasive Species Inventories (DAISIE) for Europe (<http://www.europe-aliens.org/>), the Global Naturalized Alien Flora (GloNAF) database (<https://glonaf.org/>), and the Global Biodiversity Information Facility (<https://www.gbif.org/>). These databases make important con-

tributions to the assessment of the potential of individual plant species to invade new areas (Moles et al. 2008). However, the data for particular species are limited, and multiple databases may need to be consulted. In addition, data collected by individual projects are generally not integrated into public databases (Crall et al. 2010).

A new database (InvaCost) on global economic impacts of invasive species, providing a comprehensive tool for synthesizing data on monetary costs of biological invasions, has recently been developed (Diagne et al. 2020, 2021). The database incorporates information from published reports via the Web of Science and Google Scholar, screens the reports for relevance before collating the information, and provides global cost estimates, including both economic losses and management costs attributed to invasive species (Diagne et al. 2020). Diagne et al. (2021) reported that the costs due to invasive species increased steeply from the 1970s to the present. During that time period, the minimal cost (i.e., based on reported costs only, incorporating both damage due to invasive species and costs of their control and mitigation) was \$1.288 trillion (2017 USD), amounting to an annual cost of US\$26.8 billion over the timespan, culminating in an estimated US \$162.7 billion in 2017. However, the analysis using InvaCost also revealed the paucity of reports on economic costs, including a lack of economic analyses for invasive plant costs. The authors noted that invasive plants were the third costliest taxonomic group, after invertebrates and vertebrates by several orders of magnitude. However, this likely reflected heavily on the lack of records over the period from 1970 to 2017. In this period, there were a total of 469 and 526 reports for invertebrates and vertebrates, respectively, and only 221 reports for invasive plants. The rationale for the development of InvaCost, as for the other databases mentioned previously, is to provide up-to-date, comprehensive information on invasive species impacts to inform policy-makers and the general public on the seriousness of the issue.

14.2 Challenges of Measuring Biotic Impacts of Invasive Species

Because ecological interactions are rife with complexity, biotic impacts of invasive species are difficult to measure. Types of ecological interactions potentially impacted by invasive species include herbivory, predation, competition, acting as a vector of diseases, toxic effects, hybridization, and prey for native predators (Ebenhard 1988). Note herbivory or predation is not relevant in the case of invasive plant species, but the other interactions are. Impacts of invasive species on community structure and ecosystem processes are unequivocal, documented to reduce plant species richness or the rate of nutrient cycling (Ehrenfeld 2010; Powell et al. 2011). However, measuring ecosystem functions and services is far from simple. Eviner et al. (2012) proposed a four-step process to extrapolate local and short-term measures of processes to ecosystem services: (i) specify the ecosystem processes and the related particular ecosystem service, (ii) assess other processes and their interaction to generate a given service, (iii) determine how structure and species richness affect those processes, and (iv) assess temporal and spatial variation of ecosystem services (Eviner et al. 2012).

The impacts of invasive plants depend on the mode of introduction (whether it is intentional or accidental), the form of the invasive plant (whether it is woody or non-woody), and its abundance (Blossey et al. 2001; Rai and Scarborough 2015a). Because it is difficult to ascertain long-term impacts through limited short-term research projects, studies evaluating the impacts of invasive plants either in the short run or over a small scale are seen to be flawed. Many scholars have criticized the science of invasion biology as biased, uninformative, or pseudoscientific (Davis et al. 2011; Pearce 2016; Russell and Blackburn 2017; Ricciardi and Ryan 2018). For instance, the apparent negative impacts of purple loosestrife (*Lythrum salicaria*) on wetland ecosystems, including impacts on wetland birds gleaned from superficial initial assessments, were thought to be possibly exaggerated and/or lack-

ing supporting data (Blossey et al. 2001; Lavoie 2010). Subsequent empirical research in fact indicated that some wetland bird species exhibited positive responses to *L. salicaria* invasion, whereas other bird species were negatively impacted (Tavernia and Reed 2012).

Although invasion of exotic plants may have adverse ecological impacts on recipient ecosystems, in some cases, introduction of new species may increase the functions of the recipient ecosystems. Some empirical studies have documented positive impacts on the biota and human welfare (Boltovskoy et al. 2018). Water hyacinth (*Eichhornia crassipes*) was shown to increase the abundance of micro-invertebrate and fish but decrease planktivorous fish populations (Villamagna and Murphy 2010). The impacts of invasive plants on animals and fishes were contingent on ecosystems, taxa, original community composition, and food web structure (Villamagna and Murphy 2010; Schirmel et al. 2016).

Given this context, thorough monitoring and observation of invasive plant species is required to understand their impacts. Otherwise, impacts assessed may become controversial. Studies reporting negative impacts of species, like purple loosestrife (*L. salicaria*), common reed (*Phragmites australis*), and garlic mustard (*Alliaria petiolata*), have been criticized for failing to provide sufficient supporting evidence (Blossey 1999). Such information may lead to inappropriate management strategies (Maxwell et al. 2009). Long-term monitoring of the invaded ecosystem, before, during, and after the invasion, is needed for a more comprehensive assessment of impacts (Blossey 1999).

Increasing rates of non-native species invasion call for a significant amount of resources be allotted to documenting, monitoring, and controlling invasive plants, but such efforts are not keeping pace with the demands (Diagne et al. 2021). One growing trend that may help with the lack of monitoring is the use of citizen scientists to collect invasive species data. There are several challenges associated with using citizen scientists, including wide variations in accuracy and reliability among observers and lack of clear communication channels between scientists and citizen scientists (Crall et al. 2010, 2011;

Gardiner et al. 2012). Therefore, there is a need for better training of citizen scientists and protocols for collecting data to enhance consistency.

14.3 Effects of Invasive Species on Native Plant and Animal Communities

Invasive plant species have competitive advantages as compared to native plant species and also are more productive in the absence of natural enemies (Keane and Crawley 2002; Vilà et al. 2011). They have high establishment success and exhibit rapid growth (Kolar and Lodge 2001). For instance, *Mikania micrantha* is called mile-a-minute due to its extremely rapid growth rate (Choudhury 1972; Day et al. 2016). Fast-growing vines such as mile-a-minute (*M. micrantha*) both displace and kill native plants by smothering them physically; in fact in China, one of the nicknames of mile-a-minute is “plant killer” (Holm et al. 1977; Day et al. 2016). Because they frequently possess attributes that allow them to outcompete native species, invasive species tend to dominate the recipient community and displace the native species (Ortega and Pearson 2005).

Invasive species may alter forest composition by adding new functions or ecological traits. Reduction or extinction of native plant species may occur in the invaded area, influencing ecosystem services, including provisioning, regulating, and cultural services (Crowl et al. 2008; Pejchar and Mooney 2009). The impact of invasive species on forest vegetation varies with the type of invasive species. Invasions also compromise the carbon storage capacity of forests (Peltzer et al. 2010) and permanently alter the community structure, composition, and abundance of native species (D’Antonio et al. 2001). As a result, one may observe denser canopy cover in the invaded area. Often invasive species influence ecosystem productivity by altering soil nutrients, forest fire cycles, and plant species richness. This will have pronounced effect on food web system and thus on the energy and nutrient flow in the ecosystem (Ehrenfeld and Scott 2001).

The impact of invasive species on ecosystem processes may be difficult to track over short time scales, especially when the impacts are relatively indirect. However, invasive species can potentially impact significant ecosystem properties, including geomorphological, hydrological, and biogeochemical cycles, and disturbance regimes (Westman 1990; D’Antonio and Kark 2002). Major impacts of invasive species have been observed on nutrient cycling with occasional changes in energy flow, productivity, and fire regimes as well (Simberloff 2011).

The abundance of invasive plants may result in reduced species richness and low evenness in the recipient ecosystem (Cavieres et al. 2005; Chaujar 2010). These species compete with native vegetation for light, space, soil nutrients, and moisture (Le Roux et al. 2006). They frequently outcompete native species due to their rapid growth rates (Bakker and Wilson 2001; Xu et al. 2006). In addition, some invasive species release allelochemicals (Callaway and Ridenour 2004; Xu et al. 2006), and some support soil pathogens (Mangla et al. 2008), which could inhibit the growth of native flora.

As a result of biological invasions, species composition of the invaded ecosystem will be altered. Over time, this may lead toward the homogenization of the flora and fauna (Booth et al. 2003; Ayup et al. 2014). A meta-analysis on the effects of invasive species on species richness indicated that a single invading species tended to cause a 16.6% decrease in species richness on average (Mollot et al. 2017). Plant invasions may also interfere with the evolutionary process of native species in the invaded ecosystem (Parker et al. 1999).

Invasive species alter species composition in various ways. For instance, they may alter fire cycles (Clements et al. 2001; Rossiter et al. 2003; St. Clair and Bishop 2019) and influence the course of succession (Kueffer et al. 2007). They may also reduce plant tissue nutrient contents (Pyšek et al. 2012) and pollinator visitation rates by competing with native plants (Brown et al. 2002; Totland et al. 2006). The frequent movement of pollinators between native and invasive plants may induce heterospecific pollen

transfer. This may compromise the quantity and quality of pollen and ultimately seed set (Brown et al. 2002). The effects could be more severe when species are from distant (different families) donors (Streher et al. 2020). Pollen from other species can block the stigma of recipient plants, which may reduce the reproductive capacity of the plant (Galen and Gregory 1989).

Invasive plants also influence plant-pollinator networks. They affect pollination and visitation rates, competition-facilitation, and reproductive output (Litt et al. 2014). When invasive species displace native flowering plants, they may impact the abundance of pollinators such as bees, wasps, sawflies, and ants (Lopezaraiza-Mikel et al. 2007; Morón et al. 2009; Hanula and Horn 2011). This may increase the risk of further invasion by non-native pollinators (Morales and Aizen 2002). There is also risk of hybridization due to the interaction between invasive species that are closely related to native plant species (Traveset and Richardson 2006; Schweiger et al. 2010). This may result in decreased biomass and productivity of native species (Brown et al. 2002; Totland et al. 2006; Molina-Montenegro et al. 2012).

Ecological communities are comprised of complex trophic interactions among species, which may be disrupted by the arrival of alien invasive species (Bezemer et al. 2014). The alteration of species composition, particularly in the plant community, could alter the habitat quantity and quality for animal species at multiple trophic levels (Litt et al. 2014). Because plants are primary producers, any changes to them will have direct impact on food webs. Empirical studies have demonstrated that species richness, abundance, biomass, and reproduction may be higher in native ecosystems compared to invaded ecosystems (Burghardt et al. 2009).

Invasion of native communities has significant negative impacts on herbivorous mammals that directly depend on native plants as a food source. One documented case is the impact of the invasion of mile-a-minute (*M. micrantha*) on the endangered one-horned rhinoceros (*Rhinoceros unicornis*) in Nepal (Subedi et al. 2017). Invasive plants may also modify the behavior of animals.

For example, invasion of Amur honeysuckle (*Lonicera maackii*) was reported to alter the behavior of mice and other meso-predators by altering habitat cover and food availability (Dutra et al. 2011). In addition, invasion may modify the landscape in such a way to reduce habitat connectivity, threatening both biodiversity and agricultural production (Godfree et al. 2017).

Arthropods require specific plants for food and reproduction, and incursions of invasive plants may impact specialist arthropods and decrease their abundance and taxonomic richness (Bernays and Graham 1988; Greenwood et al. 2004; van Hengstum et al. 2014). Invasive plants may provide novel resources for insects and change their foraging behavior and dispersal abilities, along with those of their predators and parasites (Bezemer et al. 2014). Dense canopies of invasive plants may disrupt insect behavior. For instance, tiger beetles (*Cicindela* spp.) and other ground species are threatened under the dense cover of invasive plants (Wagner and Van Driesche 2010). Conversely, in some cases, invasive species may serve as an important resource for the survival of insect communities (Bezemer et al. 2014). Studies have illustrated that some invasive plant species host more native insect communities compared to the native plant species (Bezemer et al., 2014). Other impacts of invasive plants on arthropods include changes in canopy, temperature and light intensity, and the soil moisture level. The new environment may affect the movement of arthropods, which is one of the major determinants of their distribution and reproduction success (Wolkovich et al. 2009). Ultimately, reduction in herbivorous arthropods will reduce the populations of higher trophic levels (Litt et al. 2014). Arthropods such as spiders, dragonflies, lacewings, mites, and flies that prey on herbivorous arthropods (Johnson and Triplehorn 2005) will also be at risk due to reduced food availability (Gratton and Denno 2005; Pearson 2009). Likewise, the abundance of parasites is likely to decrease with the invasion of exotic grasses due to the lack of host species (Simao et al. 2010). Studies have demonstrated that specialist species of moths, butterflies, and skippers (Thompson and Pellmyr 1991;

Burghardt et al. 2010), as well as species of true bugs, thrips, and beetles (Johnson and Triplehorn 2005), could decline due to the abundance of invasive plants. In addition, certain invasive plants may be toxic to larval insects (Graves and Shapiro 2003).

The impacts of invasion may be comparatively low to species at higher trophic levels compared to those within the same trophic level (Vilà et al. 2011). However, the magnitudes of the impacts depend on the feeding behavior of the species, e.g., whether they are generalists or specialists (De Groot et al. 2007). One of the greatest threats to animal species occurs via altering habitat structure (Pearson 2009). For example, purple loosestrife invasion has been associated with habitat degradation of mammals, turtles, and breeding birds (Blossey 1999). Similarly, Japanese knotweed (*Reynoutria japonica*) has had a negative impact on European wetlands, reducing the diversity and abundance of insects and wildlife (Gerber et al. 2008). The invasion of lantana (*Lantana camara*) in India affected bird habitats by altering community composition and decreased bird diversity (Aravind et al. 2010).

Invasion of alien species also provides benefits to particular faunal species. Detritivorous taxa may thrive when invasive plants are abundant through feeding on these plants and also through sheltering in decayed vegetation and ground litter (Longcore 2003; Levin et al. 2006). Similarly, invasive plants may also facilitate the movement and provide structural support for species such as spiders (Pearson 2009). Because positive impacts of invasive species are likely underreported, better assessment of positive or neutral impacts would help provide a more comprehensive picture of invasive species impacts on native plants and animals (Boltovsky et al. 2018).

14.4 Impacts of Invasive Plants on Endangered Species

Invasive species have frequently been considered to be the second greatest threat to biodiversity loss after habitat fragmentation and loss (Randall 1996; Wilcove et al. 1998), although there has

been some controversy over this claim (Davis et al. 2011). Invasive species are held to be the main cause of native species extinctions in many cases, e.g., numerous island extinctions observed to be due to invasive mammals (Courchamp et al. 2003), and most avian extinctions are ascribed to invasive species impacts (Clavero et al. 2009). Among invasive species, invasive mammalian predators are generally recognized to be the greatest threat to global biodiversity (Doherty et al. 2016). A meta-analysis by Doherty et al. (2016) indicated that 30 invasive predator species were responsible for the extinction or endangerment of 738 vertebrate species globally, amounting to 58% of all bird, mammal, and reptile extinctions. Birds with relatively small distributions are particularly vulnerable to extinction due to invasive species (Clavero et al. 2009). As mentioned in Sect. 14.3, large infestations of invasive plants such as mile-a-minute may threaten endangered species, such as the one-horned rhinoceros (Subedi et al. 2017), and other large mammals to be threatened with extinction by invasive species as well (Crooks et al. 2017).

Some argue that the negative impacts of invasive species are overestimated while failing to account for the contributions of invasive species to enrichment of biodiversity. For some commentators, invasive and native species are not categorically different, or at least not representing a clear dichotomy where every non-native species is seen as inherently harmful. Indeed, there are examples where invasive species facilitate native species populations (Rodríguez 2006). Critiques of invasion biology have claimed that non-native plants do not threaten floral biodiversity in Britain, but instead high levels of diversity of native and non-native plants are possible due to mutual compatibility (Thomas and Palmer 2015). Similarly, Dijkstra et al. (2017) demonstrated that the assemblage of invaded seaweeds has transformed habitat off the coast of Maine into a more productive two-dimensional biogenic structure, supporting two to three times more meso-invertebrate individuals and species compared to simpler forms of morphological habitat occurring at the site prior to the dominance of invasive seaweeds.

Employing the IUCN Red List for tracking endangered species, an analysis found that invasive species are responsible for the decline or potential threat to only 6% of the threatened species and less than 2% (only terrestrial plants) of the 762 extinct species globally (Gurevitch and Padilla, 2004). However, Clavero and Garcia-Berthou (2005) pointed out that the low estimate of affected species by Gurevitch and Padilla (2004) was due to how they based their calculations on the IUCN listing at the time that attributed invasive species to only 5.1% of extinctions (39 out of 762) while overlooking 129 extinct bird species with no assigned extinction cause. More recently Bellard et al. (2016) assessed the impacts of invasive species as a driver of extinction on five taxa such as plants, amphibians, reptiles, birds, and mammals. Analysis of the 215 species from five taxa reported as extinct in the 2015 IUCN Red List showed that invasive species were responsible for 58% of all extinctions in the “extinct and possibly extinct” category and 31% of all extinctions from the wild category. Based on this data, Bellard et al. (2016) concluded that invasive alien species do in fact represent the second most common cause of extinctions since AD 1500. Among the variety of viewpoints on invasive species impacts, there is a common understanding that invasive species may often influence ecosystem structure and function, which could be beneficial for some species, particularly generalists, and more frequently harmful for specialists. However, such generic statements are not helpful for policy-makers, which require more specifics on which species are severely affected or the degree to which particular invasive species are the most harmful (Gurevitch and Padilla 2004).

14.5 The Costs of Invasion

Invasive species are spreading at an increasing rate with increased international travel and trade (Perrings et al. 2002). The rate of spread is also an important determinant of how harmful the species is (Yemshanov et al. 2010). Climate change is also accelerating the speed of invasion

(Bradley et al. 2010; Diagne et al. 2021; see also Chap. 4 by Ziska in this volume). Thus, the increase in abundance of invasive species is driving up the costs associated with invasion (Pimentel et al. 2001; Diagne et al. 2021). Because invasions influence the capacity of ecosystems to supply ecosystem services, the phenomenon may have impacts on several economic sectors including agriculture, forestry, real estate, and tourism.

There are some 1297 agricultural invasive species, including insect, pests, and pathogens, worldwide (Paini et al. 2016). The impacts of invasive species on agriculture are not only an issue of economic loss but also a concern for food security. The cost of invasion has been clearly shown as increasing over time (Diagne et al. 2021). In the United States, the estimated annual value of crop loss was US\$20 billion in 1991 (USDA 2000). The annual cost of losses caused by invasive species on agriculture and forest products was almost US\$40 billion in 2005 (Pimentel et al. 2005). Similarly, 90% of the overall cost for the management of invasive plants in Australia (\$3.77 billion in 2011–2012) was on agricultural weeds (Hoffmann and Broadhurst 2016). The large agricultural producers, such as China, United States, India, and Brazil, inevitably bear the highest cost of the invasion. However, small economies such as Nepal, Cambodia, Lao PDR, Ethiopia Madagascar, Paraguay, and Guinea with agriculturally based economies are the most vulnerable to invasion (Paini et al. 2016). This is because the invasion of alien species directly impacts the livelihoods of smallholders, who are the majority in such economies (Wiggins et al. 2010). The estimated annual economic losses from the five major invasive species on mixed maize (*Zea mays*) smallholder farmers in six African nations have been reported to be between US\$0.9 and 1.1 billion (Pratt et al. 2017).

Estimating the economic value of the invasion of alien species in forest ecosystems is not straightforward because forests provide an array of ecosystem services, which are not traded in the conventional market. Information available on the damage caused by forest invasion are gener-

ally underestimated because they are calculated as the product of unit price of forest products and area affected by the invasive species (Holmes et al. 2009). However, empirical studies show that the nonmarket values of the damage or cost of invasion outweigh the market value (Olson 2006; Charles et al. 2007). Pimentel et al. (2000) estimated annual economic cost of invasive forest pests in the United States to be US\$4.2 billion, based on the assumptions of reduction in timber productivity at an annual rate of 9% and a 30% share of damage caused by invasive pests out of total damage by all forest pests. However, impacts of invasive species on nonmarket values, including recreation, aesthetic, and hydrological regulation, are not well accounted for in these types of analysis, as they fail to convert ecosystem services into monetary value (Epanchin-Niell 2017).

Invasions also affect property values in a variety of ways. In Vermont lakes, Eurasian watermilfoil (*Myriophyllum spicatum*) was shown to reduce property values by < 1–16% depending on its abundance (Zhang and Boyle 2010). The average annual marginal willingness to pay for a waterfront property on a lake free of milfoil was US\$4,179 (Olden and Tamayo 2014). In that area, the mean reduction in property value was US\$94,385. Another example of impact of invasion on property value was due to the invasion of the insect woolly adelgid (*Adelges tsuga*) and accompanying damage to hemlock forest cover on New Jersey properties (Holmes et al. 2010). Invasive knotweeds (*Reynoutria* spp.) reduce property values in Europe and North America, because of the threat they pose to structures, including their ability to break up concrete (Payne and Hoxley 2012). Estimated annual costs due to Japanese knotweed in development sites of Great Britain alone were reported to be upward of £150 million (Williams et al. 2010).

Tourism is considered a major pathway for the introduction of exotic species (Meyerson and Mooney 2007; Anderson et al. 2015). Increasing tourism activities such as infrastructure developments and recreational activities facilitates species invasion. Major tourism destinations that invasive species may affect include protected areas such as national parks, wildlife reserves,

conservation areas, heritage sites, and wetlands (Zhang and Boyle 2010; van Beukering et al. 2014; Rai and Scarborough 2015b). Invasions may often reduce wildlife populations, making wildlife sightings less frequent with concomitant adverse impacts on wildlife-based tourism (Hakim et al. 2005; van Beukering et al. 2014). Buffer zone communities situated in close proximity to parks or reserves, who rely on ecotourism, are well aware of the impacts of invasion on tourism (Rai and Scarborough 2015b). Rai and Scarborough (2015b) estimated that the loss of 1000 visitors per buffer zone household was US\$2.3 million per year. The economic loss estimated was INT. \$0.19 million per household per year after the rampant spread of invasive plant species in Ramsar sites in Pokhara valley, Nepal (Pathak et al. 2021). Note INT. \$ is a hypothetical currency calculated from local currency units utilized to standardize currency values across countries, comparing them to the purchasing power of the U.S. dollar at a given point in time. Five major invasive alien plant species responsible for the losses calculated by Pathak et al. (2021) were water hyacinth (*E. crassipes*), morning glory (*Ipomoea carnea*), southern cutgrass (*Leersia hexandra*), water lettuce (*Pistia stratiotes*), and alligator weed (*Alternanthera philoxeroides*) with *E. crassipes* being the most damaging, compromising the ecosystem services of many waterways. Invasion also reduces recreational values of activities like fishing, which is NZ\$ 44 per visit (Beville et al. 2012). At the same time, exotic game fish species are frequently introduced for recreational purposes. For example, rainbow trout (*Oncorhynchus mykiss*) has been introduced in 82 countries for sports fisheries (Cambray 2003). When there are strong economic incentives for introducing non-native species under the banner of tourism (or species introduced within recreation, agriculture, horticulture, or other sectors), it becomes very difficult to prevent such introductions even when the environmental impacts of the non-native species are well established. Plant invasion poses a serious threat to heritage sites and monuments; however, limited research is available on invasive species growing in archaeological sites and the

associated damage caused (Caneva et al. 2006; Celesti-Grapow and Ricotta 2020).

14.6 Conclusions and Future Research Needs

There is a consensus in the literature that the introduction of invasive species alters the species composition of the recipient ecosystem, which impacts nutrient cycles and primary productivity. However, the impacts of invasive species on biodiversity, society, and economy are not black and white. There is a common understanding that invasion of exotic alien species is inevitably harmful to native ecosystems; however, there are also indications that some invasive species may play positive roles in enhancing species richness and increasing the population of generalists. Some non-native species may be considered suitable for restoring degraded areas. However, it is also equally true that many invasive species adversely influence the ecological integrity of ecosystems, which may compromise the ability of ecosystems to support a diverse community of organisms at multiple trophic levels (Ruaro et al. 2018).

Quantification of the impacts by most studies of the impacts of the invasion of exotic species in different sectors is based on a number of assumptions. For instance, there is an agreement that the invasion has impact on the population growth rate (r) of native species, but direct measurement of “ r ” is rare (Park 2004). In the absence of such measurement, it is difficult to design realistic policies for the management of invasive species. Therefore, there is a need for the development of long-term monitoring and techniques to support more accurate empirical assessments of invasive species damage (see Table 14.1).

Research on costs and benefits of invasive species management are relatively scarce (Diagne et al. 2021). This is partly due to the methodological challenges associated with measuring the economic impacts of invasive species. For instance, many values associated with invasive species management are nonmarket values. There is always a challenge in valuing biodiversity and

Table 14.1 Impacts of invasive species and future research needs

Type of impact	Knowledge gap(s)	Future research needs
Biotic impacts	Lack of knowledge regarding longer-term and larger-scale impacts. Need for more information on impacts on an ecosystem level.	Long-term monitoring. Development of more systematic processes for evaluating impacts (e.g., Eviner et al. 2012).
Effects on plant and animal communities	Lack of information on how ecosystem services are impeded. Few studies illustrating indirect and long-term effects of invasive species.	More precise assessment of reductions in ecosystem services. Better assessment of indirect and long-term impacts.
Impacts on endangered species	Lack of information on impacts of specific invasive species.	Concrete assessment on how particular species or particular ecosystems featuring large numbers of endangered species are severely affected.
Costs of invasion	Lack of systematic approaches to understanding the relative importance of various modes of introduction. Relatively little information available on both costs of damage and management of invasives. Severe lack of information on costs to developing countries.	Cost of damage by the species as per their mode of introduction. Costs and benefits of invasive species management. Further development of databases such as InvaCost (Diagne et al. 2021) and specific geographic foci.

ecosystem services since the estimated values are contextual. This has created very large data gaps, particularly in terms of costs and effectiveness of control measures (Epanchin-Niell 2017). Greater collaboration between decision-makers and researchers is needed to facilitate development and communication of usable economic research in invasive species management. In the case of forest management, a better understanding of decision-making to promote forest health in the face of invasions is needed (Holmes et al. 2014). There is also a lack of information on appropriate silviculture treatments or systems for moderating the impacts of invasion and subsequent restoration of the invaded forested land (Liebhold et al. 2017).

In brief, our analysis indicates that invasion of alien species alters the structure and function of the invaded ecosystem, which also affects its capability to deliver ecosystem services. Increased economic activities including trade and tourism, coupled with the changing climate, are fueling invasion processes. Increased global plant invasions (and invasions of other taxa) have negative impacts on many economic sectors including forestry, agriculture, fisheries, tourism, and real estate, all of which primarily depend on natural resources. As stated by the International Convention on Biological Diversity in 1993 and emphasized in the second notice of the World Scientists' Warning initiative in 2017 (Ripple et al. 2017; Pyšek et al. 2020), there is an urgent need to address the impacts of invasive alien species.

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Advances in the Management of Invasive Plants

15

Katharina Dehnen-Schmutz and Ana Novoa

Abstract

Invasive plant management has moved beyond the application of conventional control methods, and new methods and approaches are constantly being developed. In this chapter, we summarize a number of recent advances in the management of different stages of the invasion process of alien plants. We discuss advances in managing the whole invasion process, such as systematic examinations (horizon scanning) to identify potential future invaders as well as management issues involving stakeholders in the development and implementation of management actions and managing pathways of introduction and spread. We also discuss advances in the management of particular stages. At the introduction stage, covering the important pathway of invasive ornamental plants, the development of noninvasive cultivars (noninvasive crop

ideotypes) could offer a management solution for some ornamental alien plants. For monitoring the establishment and spread stages, we discuss the use of technologies to analyze DNA sampled directly from the environment (environmental DNA) and detect and monitor the physical characteristics of particular areas (remote sensing) and the contributions of volunteer citizens (citizen science). At the spread stage, further technological advances are expected from editing genes (CRISPR-Cas9 gene drive) in biological control, while for some species, utilization or acceptance could offer viable alternatives. Modelling approaches are considered as a useful tool for decision-making on management actions with limited resources. Finally, focusing on increasing the resistance of ecosystems against invasive plants seems to be a promising approach for ecosystem-level management. While many of these advances have shown great potential for improving invasive plant management, we still find a lack of collection of evidence for their effectiveness in real-world applications.

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Citizen science · CRISPR · eDNA · Horizon scanning · Remote sensing · Stakeholder engagement · Utilization

15.1 Introduction

Invasive plant management encompasses planning, directing of resources, and conducting operations to prevent new plant invasions and control existing ones by eradicating them, reducing their distribution or preventing their further spread. At the most basic level, this involves the application of various classic control methods like mowing, burning, digging, slashing, felling, and applying herbicides. However, a more holistic view encompasses the whole invasion process beginning with risk assessments to prevent new invasions and culminating in management approaches that consider whole ecosystems and landscapes, and involve stakeholders at each step along the way.

This much wider management approach is essential to reduce the increasing negative impacts caused by plant invasions. The accompanying higher demand on resources must be socially justified as it can conflict with other demands on environmental management budgets. This increase in impacts and pressure on limited resources can, at least partly, be reduced through adoption of some new technological developments that have the potential to advance the management of invasive plants (Ricciardi et al. 2017; Dehnen-Schmutz et al. 2018).

In this chapter, we summarize recent advances in the management of invasive plants. We do this by looking at the different stages of the invasion process starting from the introduction to the establishment and spread stage. We also discuss advances that are relevant to the invasion process as a whole, such as the need for greater stakeholder involvement or modelling methodologies (Fig. 15.1).

15.2 Horizon Scanning

Horizon scanning is known as “the systematic examination of potential (future) problems, threats, opportunities and likely future developments, including those at the margins of current thinking and planning” (van Rij 2010). While different approaches can be used for horizon scan-

ning, it usually consists of collecting a large set of data and reducing it to a subset of the most important data that should be prioritized, often involving expert consultation.

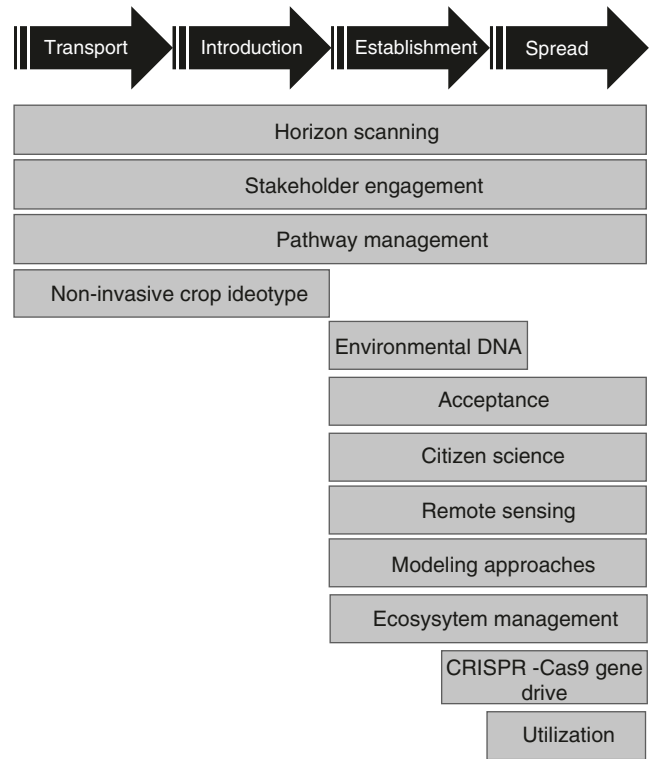
Horizon scanning has been proven useful for identifying potential invasive species (Roy et al. 2014) and their pathways of introduction (Matthews et al. 2017), as well as for identifying issues that are likely to affect future management of invasive species (Ricciardi et al. 2017; Dehnen-Schmutz et al. 2018).

New tools could help improve future horizon scanning exercises, such as the use of supervised natural language processing tools for retrieving information from the massive body of scientific literature published on invasion science (Tshitoyan et al. 2019) or by media monitoring, as it is done for emerging plant health threats by the European Food Safety Authority (Alomar et al. 2016).

15.3 Stakeholder Engagement

Stakeholder engagement is the process of involving all those who may be affected by or can influence the implementation of the management actions, e.g., decision-makers, organizations that help implement management actions, or industries that commercialize alien species (Carroll et al. 2016). Engaging stakeholders in the management of invasive plants can help in understanding their perceptions, identifying valuable local knowledge and practices, promoting awareness and social learning, reaching consensus and gaining support, formulating co-management programs, and dealing with potential conflicts of interest (Shackleton et al. 2019; see Fig. 15.2). For example, local communities in Nepal prioritized invasive plants for management according to their impacts following focus group discussions (Shrestha et al. 2019). On the other hand, the lack of stakeholder involvement and support can hinder management actions (García-Llorente et al. 2008). Therefore, the need for stakeholder engagement has been stipulated in several management strategies around the world (e.g., Environment Canada 2004; Brundu and

Fig. 15.1 Advances in the management of the different stages of the invasion process of alien plants. Black arrows indicate the different stages of plant invasions. Gray boxes indicate the advances in management discussed in this chapter



Richardson 2016), and research on the topic has increased over the last decade (Shackleton et al. 2019).

Novoa et al. (2018) proposed a framework that includes steps that can be followed and techniques that can be applied to engage stakeholders in issues related to the management of alien species. Although some of the steps have already been implemented (Novoa et al. 2016), this framework still needs to be tested for wider applicability.

15.4 Pathway and Vector Management

The management of introduction pathways of alien plants is one of the most effective measures to prevent new invasions and the increase in abundance of existing invasions. Here, the management of international pathways through trade regulations and international agreements plays a crucial role (discussed in Chap. 3 of this volume). However, pathway management is also one of the

important steps at the national and regional scale to prevent the introduction and spread of species to new sites. Various measures are necessary to target either pathways of accidental introductions and spread or pathways of deliberate release of invasive or potentially invasive alien plants. Accidental introduction of plants to new sites occurs through transport of propagules during different human activities, such as the introduction of propagules or plant material attached to machinery, seeds included in soil (e.g., potted plants, growing media), or plant segments or seeds attached to humans or animals. However, these accidental introduction pathways are rarely managed.

High numbers of viable seeds of invasive species are dispersed by vehicles (Ansong and Pickering 2013). Attempts to manage this pathway have been mainly applied to vehicles after they were used in invasive plant management operations or when entering and leaving conservation areas. For example, in Queensland, Australia, there are washdown facilities for cleaning vehicles that pass through areas of



Fig. 15.2 Stakeholders discussing the potential implementation of management actions aiming at preventing the introduction of invasive cacti (family Cactaceae) in South Africa

high abundance of parthenium weed (*Parthenium hysterophorus*). A recent analysis has shown that large numbers of viable seeds can be successfully removed in these facilities (Bajwa et al. 2018). However, this methodology may not be practical in areas with higher volumes of traffic. In such areas, roadside vegetation management could be employed to prevent the attachment of propagules to vehicles. Another example is a model based on experimental evidence developed by Lommen et al. (2018). Considering growth stage, seed bank survival, and costs, this model devises an optimal mowing regime for preventing further spread of *Ambrosia artemisiifolia* along roadsides. The current lack of research in the link between roadside management and the dispersal of species (Bernes et al. 2017) is of concern for the development of strategies preventing the spread of invasive plants by vehicles.

Seeds used for feeding birds are also a well-known pathway of introduction and dispersion of alien plants. Seeds of invasive plants can be either deliberately used as bird seed or accidentally be included in birdseed as contaminants from places where the birdseed is cultivated (Hanson and Mason, 1985). Heat treatment has recently been shown as a successful classical methodology to devitalize germination ability of birdseed (Blythman and Sansom 2019).

The main pathways for plant invasions globally are the deliberate introduction and cultivation of alien plants for ornamental use, agriculture, or forestry (van Kleunen et al. 2018). Increased efforts are required for effective pre- and post-border risk assessments that are supported by verifiable industry codes of conduct, cost-sharing agreements, and other types of legal responsibility (Hulme et al. 2018) along with initiatives to raise consumer awareness and initiate behavioral changes. A fur-

ther option is the development of noninvasive cultivars to close this pathway (Sect. 15.6).

15.5 Modelling Approaches

Increasing numbers of academic research outputs are demonstrating the usefulness of modelling approaches to devise best management strategies for invasive plants. Results from models providing predictions on future establishment and spread of invasive plants, often under climate change scenarios, are informing risk assessments and are underpinning policies to regulate or ban the trade of high-risk species. Novel modelling approaches such as extreme learning machine models are also being used to detect new invasions by improving image recognition of invasive species (Demertzis and Iliadis 2017). For existing invasions, modelling approaches are particularly useful to support managers' decisions on how to allocate the often-limited budgets to different management actions. The best management approach also depends on the life history of the invading plants. For example, Hoffberg et al. (2018) developed a model to support management decisions on whether to allocate budgets to either reduce the abundance of invasive plants in heavily invaded areas or to aim for eradication by re-treating previously controlled smaller populations at the regional level. While many of these approaches look promising, evidence of the use of modelling at the local level and in practical management actions undertaken by land managers seems to be rare.

Modelling approaches can also be used to inform policy decisions for invasive plant management, and this is particularly the case for economic models. This has been investigated, for example, for the application of taxes on newly introduced ornamental plants in North America (Barbier et al. 2011), or tariffs on goods carrying risks of accidental introductions (McAusland and Costello 2004). However, the implementation of such economic instruments

has not yet taken place due to the lack of support from stakeholders as well as challenges in the practical application and data requirements (Barbier et al. 2013).

15.6 Noninvasive Crop Ideotype

From the eighteenth and nineteenth century onward, so-called plant hunters have travelled the world to find new plant species first for botanical collections but increasingly also for their commercial ornamental use, therefore focusing on those species that present an initial suite of attractive characteristics. Often, public and private sector plant breeders manipulate the genetic patterns of the collected plants to produce cultivars with higher market value (van Kleunen et al. 2018). Usually, only traits improving fitness (e.g., faster growth, disease resistance, or frost tolerance) or aesthetics of the plants (more colorful or bigger flowers) are selected. However, some breeders also select traits that help to create noninvasive crop ideotypes (Anderson et al. 2006).

A noninvasive crop ideotype consists of one or a set of desirable traits that outline breeding objectives to create noninvasive cultivars. Anderson et al. (2006) proposed several traits for incorporation into noninvasive crop ideotypes, including lack of seed germination, elimination of asexual propagules, or lack of pollinator rewards. An example of such ideotypes is *Euonymus alatus*, a popular ornamental plant species that was introduced to the United States from Asia in the 1860s. This species can produce up to 50,000 seeds per plant per year and spreads rapidly, replacing native vegetation. However, Chen et al. (2008) developed a sterile cultivar which neutralized the invasiveness of *E. alatus*.

Regardless of the selected traits, it is important to determine whether transformed individuals offer reliable trait stability. For example, *Opuntia ficus-indica*, a spiny cactus species native to Mexico, is recorded as invasive in many parts of the world (e.g., Australia, Ethiopia, and South Africa). However, the noninvasive spineless cultivar of *O. ficus indica* presents all the benefits of the original spiny forms. The plants

can be used, especially in arid areas, as fodder for animals and as a source of fruit and have the advantage of being noninvasive. Spineless types are browsed by various herbivores, hence regulating the population. However, experimental evidence (Novoa et al. 2019) suggests that, when reproducing by seed, the spineless cultivars of *O. ficus indica* might revert to the spiny forms and lead to future invasions.

Despite the potential benefits of developing noninvasive crop ideotypes, only a few breeding programs include noninvasiveness as an objective. Most of such breeding programs belong to the public sector – e.g., breeding programs launched by the University of Minnesota (Anderson et al. 2006) or the US National Arboretum (Egolf 1988). However, interest is growing among breeders, wholesalers, or retailers (Anderson et al. 2006). Increasing the interest of all actors in such programs is crucial for reducing the risks of invasion while retaining market value of new plant releases.

15.7 Remote Sensing

Remote sensing is the process of collecting data about the Earth, usually from aircrafts or satellites. Since the 1970s, remote sensing has been an important tool for the management of invasive plants: it has been used for early detection, to identify invasions, predict their future distribution, and assess their impacts (Vaz et al. 2019).

Recent technological advances are making remote sensing techniques more accurate and efficient than ever before. For example, the multispectral scanner of Landsat 1 (the first Earth-observing satellite launched in 1972 to monitor and study the Earth's landmasses) provided multispectral views of the Earth's surface at a ground resolution of approximately 80 m (Acker et al. 2014). Nowadays, the Dove satellites (operated by Planet in San Francisco, California) offer data at a resolution of 3.7 m (Kwok 2018). Moreover, researchers can now browse free remote sensing data at online portals such as the European Space Agency's Copernicus Open Access Hub, NASA's Earthdata Search, or Google Earth. Unmanned

aerial vehicles (i.e., drones) have also become easier to obtain and use (Lorah et al. 2018), also providing further potential for citizen science. Furthermore, numerous tools are constantly being developed to access and analyze remote sensing data (e.g., Murray et al. 2018; Neeley 2018). These advances are improving the capacity of remote sensing to support invasive plant management actions (Vaz et al. 2019).

Until recently, remote sensing techniques have been mainly used to study already established plant invasions (He et al. 2011). However, the potential uses of remote sensing techniques to manage the introduction and establishment stages of the invasion process are increasingly being discussed (e.g., Larson et al. 2020).

15.8 Environmental DNA Metabarcoding

Environmental DNA (eDNA) is DNA that, instead of being sampled directly from an organism, is sampled from the environment (e.g., from soil or water). Organisms (dead or alive) leave traces of their genetic material such as dead skin, gametes, or feces in their surrounding environment. When analyzing eDNA, these traces are identified and used to detect the presence of certain organisms in a particular habitat (Deiner et al. 2017). Therefore, eDNA metabarcoding is a promising tool for detecting the presence of invasive species during the early stages of the invasion process (Simmons et al. 2015).

Until now, eDNA metabarcoding has mainly been used for detecting the presence of invasive animals in aquatic and terrestrial ecosystems (e.g., Mauvisseau et al. 2018; Williams et al. 2018). However, recent studies have shown that eDNA metabarcoding techniques can also be effective in detecting the presence of invasive plants in aquatic ecosystems (Scriver et al. 2015).

eDNA metabarcoding currently has some drawbacks for detecting the presence of invasive species (e.g., it might capture signals from dead organisms or have false-positive or false-negative readings). However, it is expected to improve over time (e.g., through improving eDNA collec-

tion and extraction methodologies, optimizing bioinformatic pathways, expanding reference databases, or engaging citizens in the collection of eDNA) and emerge as an essential powerful tool for the management of invasive species (Ruppert et al. 2019).

15.9 Acceptance of Invasive Plants

There are several reasons why it is not possible to manage invasive plants in every location. First, the scale of invasions is now beyond complete human control. Therefore, the available resources and pragmatic trade-offs are guiding decisions on which species to control and which to accept while also acknowledging that the return of many habitats to pristine pre-invasion status is not feasible (Head et al. 2015). Second, managers face trade-offs for invasive plant species that provide considerable benefits for agriculture, forestry, or aesthetics because of their associated sociocultural values. Examples of such include the large-sized old specimen of the alien *Eucalyptus diversicolor* trees in the Table Mountain National Park in South Africa, popular with hikers, cyclists, and tree enthusiasts. Aiming to support management decisions for invasions facing these trade-offs, a support framework has been developed to guide managers on a case-by-case basis (Gaertner et al. 2017). Third, invasive plants are part of new species assemblages in novel ecosystems that have been created through human impacts but are not dependent on human maintenance. In some cases, these novel ecosystems are the result of irreversible changes caused by invasive species (Hobbs et al. 2006). In these ecosystems, impacts associated with invasive plants elsewhere may not occur. Provided they are not constituting a risk, they can provide similar levels of ecosystem services as native ecosystems. For example, they can play an important role for the health and social well-being of urban residents in cities (Kowarik 2011).

15.10 Citizen Science for Early Detection and Monitoring of Plant Invasions

Laypersons have been involved in the recording of alien plant species for a long time. For example, since the early 1960s, amateur botanists have been systematically recording plants, including aliens, in the British Isles to create distribution maps of the British flora (Pescott et al. 2015). The potentially crucial role of citizen science for early detection and monitoring of invasive plants has only become apparent over the last decades and with the increasing use of record-taking through the Internet and smartphone applications. Citizen scientists, defined here as volunteers contributing to either data collection or data analysis of a clearly defined research hypothesis (ECSA 2020), can be involved in the management of plant invasions at several stages of the invasion process: in particular, for early detection of species from an alert list as well as the reporting of occurrences of high-impact species to initiate and support management actions. Examples are listed in Table 15.1. A recent pilot study also demonstrated that citizen science is a useful approach to identify potentially invasive ornamental plants before they even start spreading outside gardens (Dehnen-Schmutz and Conroy 2018), and the approach has now been implemented on a permanent basis for the United Kingdom and Ireland in the Plant Alert project (see Table 15.1). However, a major problem for many citizen science projects is the often-limited time for which funding is available, which can make it difficult to maintain the engagement of citizen scientists. Project-specific smartphone apps often require costly updates to continue their listing in the app stores. The PlantTracker app, for example, was used to record 20 high-priority invasive plants in Britain, and it received more than 20,000 records. However, it had to be withdrawn from the app stores because of lack of funding.

Table 15.1 Examples of citizen science projects for invasive alien plant management

Project	Species recorded	Country/ Region	System	Organization	Web page
<i>Invasive Alien Species in Europe</i>	49 EU listed species of union concern (including 23 plants)	European Union	Mobile phone app	Joint Research Centre, EU Commission	https://easin.jrc.ec.europa.eu/easin/CitizenScience/BecomeACitizen
<i>Invasoras.pt</i>	Invasive plants in Portugal	Portugal	Mobile phone app and web-based	Escola Superior Agrária de Coimbra and Centre for Functional Ecology, University of Coimbra	https://invasoras.pt/
<i>Plant Alert</i>	Potentially invasive ornamental plants in gardens	United Kingdom and Ireland	Web-based	Botanical Society of Britain and Ireland, Coventry University	www.plantalert.org
<i>PlantTracker</i>	Distribution mapping and early detection of 20 high-priority invasive plants	United Kingdom	Mobile phone app	UK environmental agencies	www.plantracker.org.uk
<i>Ambrosia SCOUT</i>	Recording <i>Ambrosia artemisiifolia</i> to help control efforts	Germany	Mobile phone app and web-based	Federal Ministry for the Environment	http://ambrosiascout.de/
<i>Wild Spotter</i>	Lists of invasive species to record which are specific to 24 “wild places”	United States	Mobile phone app	University of Georgia, USDA, and partners	https://wildspotter.org/index.cfm
<i>Invaders of Texas</i>	141 invasive plants	United States	Web-based	Partnership local authorities, stakeholders	www.texasinvasives.org

Citizen science methods also link very well with several other management approaches discussed in this chapter. A study in Portugal demonstrated how data on the distribution of invasive *Acacia* species collected within the citizen science project Invasoras.pt. (see Table 15.1) could be successfully combined with data collected by researchers to improve surveillance and species distribution models (Sect. 15.10) (de Sá et al. 2019). Similar, future projects could work with citizen scientists using drones for remote sensing (Sect. 15.7) or participating in projects using eDNA (Sect. 15.6) (Larson et al. 2020).

15.11 Ecosystem Management

Managing ecosystems to increase resistance against invaders is an approach based on theories of functional and community ecology. Opportunities for invasions arise in communities where a suitable niche is provided by the availability of resources, the presence/absence of natural enemies, the physical environment, and interactions between these factors (Shea and Chesson 2002). So far, functional ecology approaches have mainly been tested experimentally in pot and field experiments with the ultimate goal to design a framework for the creation of native plant covers resistant against re-invasion after the removal of invasive plants (Byun et al. 2018). For example, Yannelli et al. (2018) tested an experimental mixture of native grassland species with similar traits as introduced alien plants to increase resistance to their invasions but found that mixtures of fast-growing species sown at high densities were more effective in suppressing growth of invaders than mixtures of species with similar functional traits. Other experiments have explored manipulating resource availability to prevent reestablishment of invasive plants. However, in experimental sites in Minnesota, USA, the reestablishment of *Phalaris arundinacea* only partly decreased where soil nitrogen availability was reduced through sawdust incorporation in the soil and follow-up treatments would still be necessary (Iannone III and Galatowitsch 2008). Reducing nutrient availability and shading of aquatic habitats by tree planting have been proposed to manage

invasions of aquatic plants (Hussner et al. 2017). At a landscape scale, functional ecology approaches are also useful to manage plant invasions. For example, for frugivore-dispersed invasive plants, strategically placed perches for birds can be used to provide seed sinks where the germination and establishment of invasive plants could be managed (Buckley et al. 2006).

15.12 CRISPR-Cas9 Gene Drive for Improving Biological Control

Classical biological control (i.e., controlling invasions by using introduced, highly selective natural enemies) has been used for centuries as a tool to manage plant invasions. Although it has always been criticized due to its potential non-intended effects (e.g., causing non-target species to become extinct), the benefits of biological control are significant (Van Driesche et al. 2010). For example, the aquatic weed *Azolla filiculoides* has been successfully controlled in South Africa since a weevil, *Stenoplemus rufinatus*, was released in 1997 (Schaffner et al. 2020). If appropriate pest risk analysis is followed, such risk can be minimized (Suckling and Sforza 2014). The International Standard for Phytosanitary Measures provides guidelines for performing such risk analysis (Kairo et al. 2003).

CRISPR-Cas9 gene drive is a recent technology that can be used to edit genes. As such, this technology has been proposed for improving the effectiveness and reducing the risks of biological control (Webber et al. 2015). For example, CRISPR-Cas9 can be used to eliminate undesirable traits found in biological control agents such as flight or diapause or reduce fecundity (Gurr and You 2016). However, as Webber et al. (2015) pointed out, CRISPR-Cas9 gene drive has the ability to drive species to extinction and could turn into a global conservation threat; therefore, there is an urgent need to develop a transparent regulatory framework in collaboration with stakeholders and scientists from different disciplines.

15.13 Utilization

In certain cases, promoting the use of invasive plants (e.g., as food or biofuel) can help to reduce or control their populations (Pasko et al. 2014). For example, in South Africa, where the invasion of *Opuntia ficus-indica* is successfully managed using biological control, the remaining isolated infestations are being controlled through utilization, mainly for human consumption (Beinart and Wotshela 2003). In China, *Ambrosia artemisiifolia* and *Conyza canadensis* have been experimentally used for making biochar, which proved then very effective as adsorbents of heavy metals from wastewater (Lian et al. 2020). Utilization could therefore be a feasible approach, in particular, as both species are widespread in China and due to multiple herbicide resistances are increasingly difficult and expensive to control with traditional methods (Lian et al. 2020).

However, all utilization initiatives should be carefully planned (De Lange et al. 2012) since promoting utilization has the risk of creating dependencies and could incentivize the growth of the target invasive plants. If people derive benefits from invasive plants, they may facilitate their growth rather than control it, and it may be best to provide a regulatory framework in which such initiatives could take place.

15.14 Conclusions

This review provides a summary of recent advances in the management of invasive plants. Despite some of them being more popular than others among the research community (e.g., remote sensing compared to noninvasive crop ideotype), the number of scientific publications discussing most of these advances has grown markedly over the last decade (Fig. 15.3). The only exceptions are the apparent recent loss of interest in the development of noninvasive crop ideotypes and few current publications on the topic of pathway management. These observed trends might, however, be a result of biases during our literature search (see Fig. 15.3 for details on the search terms used) and can also change in the future as new advances are devel-

oped. Nevertheless, it is interesting to see how a number of publications dealing with certain advances, such as horizon scanning, stakeholder engagements, or the use of eDNA and gene drive techniques, show an exponential growth, suggesting their popularity and therefore potential for improvement.

The 12 advances presented in this chapter are constantly being improved, and they present a promising potential for advancing the management of plant invasions. However, some of them currently require large amounts of capacity, funding, and time (e.g., stakeholder engagement, remote sensing, and citizen science). As a consequence, many stakeholders doubt that the necessary resources for implementing such advances would be available, given their concerns about lack of or future decline in resources for the management of invasions (Dehnen-Schmutz et al. 2018). Furthermore, for many of the advances introduced here, we found a lack of systematic collection of evidence for their application in real-world settings. In some cases, however, this could be due to their only recent development, and therefore, it may hopefully change over time. To enable their wider application and accessibility to land managers and decision-makers beyond the research community, increased efforts in collecting such evidence and communication of the findings are needed.

It is important to note that the overview of the advances in the management of plant invasions presented here does not aim to be exhaustive and therefore does not include all existing advances. For example, an important advance not discussed in this chapter is the creation of collaborative global networks (Packer et al. 2017) or global working groups (Novoa et al. 2019), which can help avoid duplicating research efforts and reduce management costs, since sharing lessons gained from successes and failures of managing particular invasions in one country can guide managers in others (see Chap. 16). International standards (e.g., EPPO 2014) and codes of conduct (Hulme et al. 2018) are also important advances not included in this chapter. A wide array of tools is also being developed to help prioritization, risk assessment, and pest/pathways risk analysis. An example of these tools is the EICAT scheme,

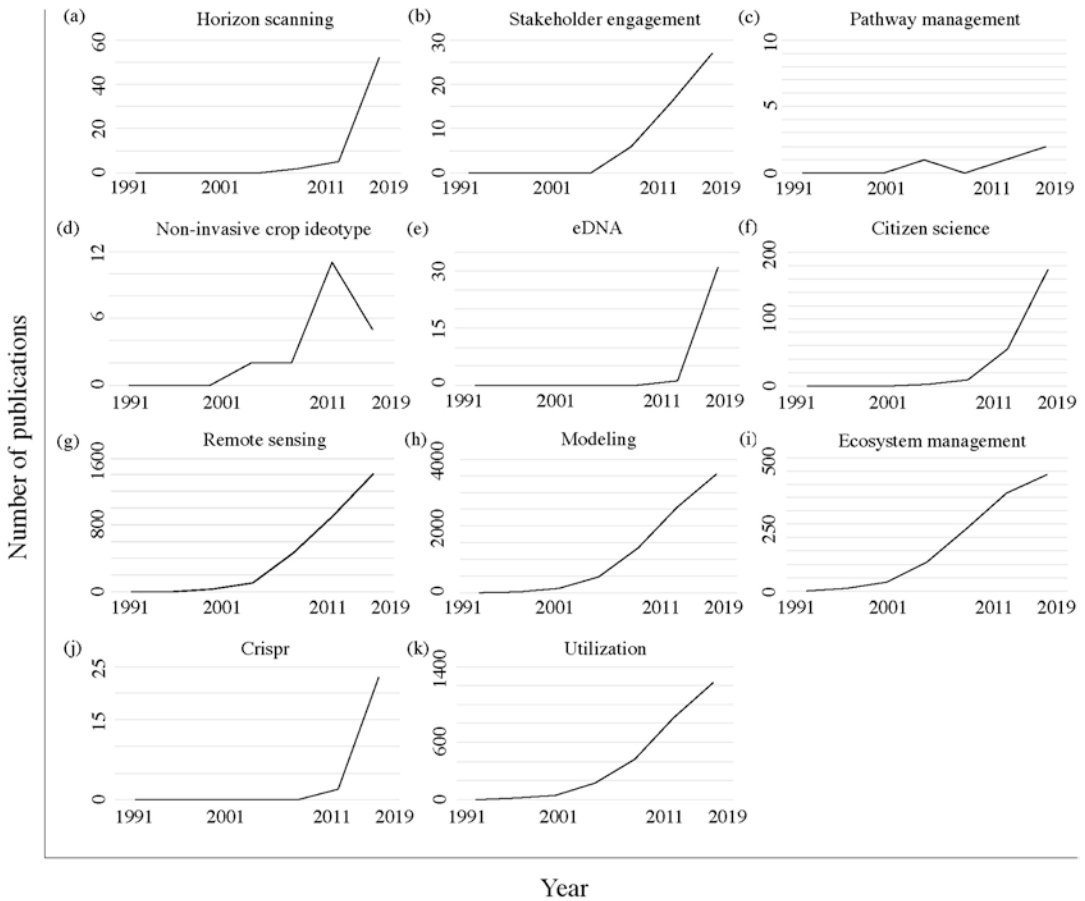


Fig. 15.3 Trends in peer-reviewed publications dealing with recent advances in the management of invasive plants over time. The data is based on results from an ISI Web of Science search using the following research terms: (a) “horizon scanning” AND “invasive plants”, (b) “stakeholder engagement” AND “invasive plants”, (c) “pathway management” AND “invasive plants”, (d) “modelling” AND “invasive plants”, (e) “non-invasive crop idotype”

AND “invasive plants”, (f) “remote sensing” AND “invasive plants”, (g) “eDNA” AND “invasive plants”, (h) “citizen science” AND “invasive plants”, (i) “ecosystem management” AND “invasive plants”, (j) “crispr” AND “invasive plants”, and (k) “utilization” and “invasive plants”. Advances in acceptance were not included in this search since the papers discussing these could not be picked up by a simple search on ISI Web of Science

which has been recently adopted by the IUCN as an objective and transparent method to classify alien taxa according to the magnitude of their environmental impacts (Kumschick et al. 2020). Moreover, culturomics (i.e., the study of human interactions with nature through the quantitative analysis of digital data) has also been recently proposed as a novel tool with great potential to inform invasion science and practice (Jaric et al. 2021). In 2017, a horizon scanning aimed at identifying emerging issues for conservation and biological diversity (Sutherland et al. 2017)

discussed the potential use of robotic technologies to eradicate and control marine invasive species. Although these technologies are currently often prohibitively expensive, robots can work longer hours and at greater depths than human divers and therefore can be more effective at managing biological invasions. These techniques could potentially be also applied to manage plant invasions in many circumstances.

The advances presented here, as well as the many others not discussed in this chapter, should not be seen in isolation. Instead, these methods

should be integrated when designing management actions and strategies and should be adapted as the management is implemented. In this context, applying adaptive management theory (acknowledging uncertainty and its effect on decision-making while seizing opportunities to reduce this uncertainty) to the management of invasive plants has attracted substantial interest during the last decade (Foxcroft and McGeoch 2011; Rout et al. 2017; Lambin et al. 2020).

Overall, a wide array of new methodologies, theories, and techniques are quickly advancing our ability to prevent, eradicate, and control invasive plants. The integration of these advances together with existing classic management methods in invasive plant management strategies can represent a more efficient and effective use of the often-scarce resources available to manage invasive plants.

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Moving Toward Global Strategies for Managing Invasive Alien Species

16

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Abstract

As human communities become increasingly interconnected through transport and trade, there has been a concomitant rise in both accidental and intentional species introductions,

resulting in biological invasions. A warming global climate and the rapid movement of people and vessels across the globe have opened new air and sea routes, accelerated propagule pressure, and altered habitat disturbance regimes, all of which act synergistically to

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trigger and sustain invasions. The complexity and interconnectedness of biological invasions with commerce, culture, and human-mediated natural disturbances make prevention and management of invasive alien species (IAS) particularly challenging. Voluntary actions by single countries have proven to be insufficient in addressing biological invasions. Large gaps between science, management, and policy at various geopolitical scales still exist and necessitate an urgent need for more integrative approach across multiple scales and multiple stakeholder groups to bridge those gaps and reduce the impacts of biological invasions on biodiversity and human well-being. An evidence-based global strategy is therefore needed to predict, prevent, and manage the impacts of IAS. Here we define global strategies as frameworks for evidence-based visions, policy agreements, and commitments that address the patterns, mechanisms, and impact of biological invasions. Many existing global, regional, and thematic initiatives provide a strong foundation to inform a global IAS strategy. We propose five recommendations to progress these toward global strategies against biological invasions, including better standards and tools for long-term monitoring, techniques for evaluation of impacts across taxa and regions, modular regulatory frameworks that integrate incentives and compliance mechanisms with respect to diverse transcultural needs, biosecurity awareness and measures, and synergies with other conservation strategies. This proposed approach for IAS is inclusive, adaptive, and flexible and moves toward global strategies for better preventing and managing biological invasions. As existing research-policy-management networks mature and others emerge, the accelerating need for effective global strategies against biological invasions can finally be met.

Keywords

Globalization · Frameworks · Networks · Policy · Regulation · Stakeholder engagement

16.1 Introduction: A Global Approach to a Global Challenge

Vast shifts in biodiversity are occurring in nearly every ecosystem as increasing global interconnectedness and the inexorable warming of land, aquatic, and ocean habitats due to human-caused climate change give rise to more biological invasions and the poleward movement of uncounted (and uncountable) species (Sorte et al. 2010; Bates et al. 2014; Hulme 2017; Seebens et al. 2017; Pyšek et al. 2020). People and products are moving ever more rapidly between global transport nodes, often with organisms as both intended and unintended passengers that readily survive these journeys and quickly become established within new territories. Human-modified habitat disturbance often aids both their movement and establishment. As thousands or tens of thousands – or more – species invade communities composed of both native and previously introduced plants and animals, we expect profound shifts in ecological networks, trophic dynamics such as predator-prey regimes, and virtually every other aspect of ecosystem structure and function.

Much less predictable, but perhaps increasingly powerful, extreme weather events (e.g., cyclonic storms and floods) or natural disasters such as tsunamis can also redistribute materials and organisms into highly disturbed and far-flung environments. For example, with constantly growing and expanding human populations, natural disasters have far greater probabilities of unexpected, and perhaps unpredictable, consequences relative to species dispersal and thus invasions. Since the 1950s, the mass production of styrene, fiberglass, and other plastic products – from food packaging to household goods to automobiles – has become a dominant component of our waste streams. Vast amounts of plastic are concentrated in megacities, many of which are located on or near the coasts. This largely non-degradable material ultimately ends up in estuaries and seas and gets further distributed globally. In March 2011, the Great East Japan Earthquake and Tsunami swept away cities and towns,

including ports, harbors, and aquaculture farms, on the Pacific coast of northern Honshu, with water currents carrying millions of plastic, metal, and wood items forming marine debris. Prior to that, the last major tsunami in the region occurred in 1933 – before the plastic era. The associated debris did not act as a vector for invasive species as the plastic debris associated with the recent tsunami did. In 2012, the debris field from Japan began to arrive in North America and the Hawaiian Islands. A relatively small sample (634 items) of the landed debris revealed that nearly 400 living Japanese marine species had successfully crossed the North Pacific using debris as dispersal agents (Carlton et al. 2017, 2018). By 2013–2014, the debris field consisted almost entirely of plastic objects (the wood having been destroyed by shipworms and most metal products having sunk) (Treneman et al. 2018). As of 2018, debris with living Japanese species continued to travel far and wide. The proliferation of a non-biodegradable substance at the land-sea interface, susceptible to movement by tsunami or the increasing number and strength of human-mediated storms, has thus created a passive novel vector for long-distance dispersal of species – with much greater spatiotemporal longevity than ever witnessed in nature (Carlton et al. 2017, 2018). This is a prominent example in the Anthropocene of the increased opportunities for invasive organisms and novel vectors, including passive unintentional transport, available to spread into regions where they never previously occurred. Such new dimensions of the global invasion problem call for innovative solutions.

While globalization has been underway for centuries and has intensified since the period of “great acceleration” of the 1950s, invasion science has been unable to halt the introduction, spread, and ecological, economic, and human health impacts of invasive alien species (IAS) around the world (Seebens et al. 2017). Our knowledge and awareness of the threats posed may be growing, but our global capacity to reverse trends and prevent and minimize impacts is limited in the absence of a better strategic vision, globally coordinated efforts, and legally binding targets. Similarly, although knowledge available

on the threats invasive species pose has exponentially increased since the late 1980s (Pyšek and Richardson 2010; Vilà et al. 2010; Pyšek et al. 2012; Ricciardi et al. 2013; Gaertner et al. 2014; Table 16.1), large gaps still exist between science, policy, and management. There is thus an urgent need for more integrative approach, across multiple scales and stakeholder groups, to bridge these gaps and reduce the impacts of biological invasions on biodiversity and human well-being. In a globalized world, how countries manage invasive alien species is critical to prevention, including how donor and recipient countries coordinate efforts to reduce introductions of new invaders (see Glossary, Box 16.1). Undoubtedly, differences in wealth among countries and the ability to build institutional capacity for international cooperation can limit coordination (Early et al. 2016; Latombe et al. 2017). Large mismatches may occur across borders in national legal or regulatory frameworks (Nuñez and Pauchard 2010), and these need to be considered when formulating global approaches. More research is needed to better understand how IAS introductions and impacts differ between developed and developing countries and whether smaller economies have fewer IAS introductions. Regional, bilateral, and multilateral regulatory instruments, including the Convention on Biological Diversity (CBD), have emphasized the need to prevent the movement of IAS. Lesser developed countries may not have the resources, technology, or capacity to develop comprehensive quarantine measures, but they may have lower levels of invasions due to lower introduction efforts and lower historic trade (Nuñez and Pauchard 2010). However, other imbalances may exist between trading partners, where the partner with less influence and capacity may not be empowered to enforce safeguarding regulations or restrict imports that present a risk for species introduction. While preventing export in the first place would be ideal, all nations are already overburdened to prevent importing IAS, and what leaves a country’s jurisdiction is beyond the management and regulatory capacity of even the most advanced countries in the world. Given this scenario, local actions need to be well-coordinated with global strategies to be more effective

Table 16.1 Existing networks: knowledge

Acronym	Full name	Stated purpose	Spatial scale	Temporal scale	URL
AS	Alien scenarios	Develop the first global, continental, and regional scenarios and models for biological invasions in twenty-first century Assess the effectiveness of regulations for invasive alien species Evaluate the future impacts of biological invasions on environment and livelihoods	Global	1 year (2019–ongoing)	alien-scenarios.org/
EICAT	Environmental impact classification of alien taxa	1. Identify taxa that have different levels of environmental impact 2. Facilitate comparisons of the level of impact among regions and taxonomic groups 3. Facilitate predictions of potential impacts in target region and elsewhere 4. Prioritize management actions 5. Evaluate management methods	Global	5 years (2015–ongoing)	iucn.org/theme/species/our-work/invasive-species/eicat
GUBIC	Global urban biological invasion consortium	To uncover how urbanization shapes, and is shaped by, movement of species around the world. Focuses on how environment, city structure, biogeography, history, trade, economics, and governance all shape biodiversity and its benefits in cities	Global	2 years (2018–ongoing)	utsc.utoronto.ca/projects/gubic/
ICES	International Council for the Exploration of the Sea	To advance and share scientific understanding of marine ecosystems and services they provide and to generate advice for conservation, management, and sustainability goals	Global	118 years (1902–ongoing)	ices.dk/
InvasiBES	InvasiBES: Understanding and managing the impacts of INVASive alien species on biodiversity and ecosystem services	InvasiBES aims to better understand and anticipate multifaceted impacts of invasive alien species on biodiversity and ecosystem services and to provide tools for their management. It combines primary data and models across habitats (terrestrial, freshwater, and marine) and scales (continental and local)	Multi-continental (EU, United States)	3 years (2019 to 2021)	elabs.ebd.csic.es/web/invasibes
MIREN	Mountain invasion research network	To understand the effects of global change on species' distributions and biodiversity in mountainous areas	Global	15 years (2005–ongoing)	mountaininvasions.org/

Acronym	Full name	Stated purpose	Spatial scale	Temporal scale	URL
NEON	National Ecological Observatory Network	To collect and provide open data that characterize and quantify complex, rapidly changing ecological processes	Continental (USA; 48 lower states, HI&PR)	8 years (2012–ongoing)	neonscience.org/
SEICAT	Socioeconomic impact classification of alien taxa	<ol style="list-style-type: none"> 1. Identify the magnitude of socioeconomic impacts of alien taxa. 2. Consider context dependency of impacts and comparisons among regions and taxa. 3. Facilitate predictions of potential impacts in the target region and elsewhere. 4. Aid in prioritization of alien taxa and relevant introduction pathways for management actions. 	Global	18 months (2018–ongoing)	Bacher et al. (2018)

Box 16.1 Glossary of Terms

Common gardens:	Experiments conducted either in the field or greenhouse in order to test for differentiation among any set of genetically distinct plant groups in a relatively homogeneous environment
Donor regions:	Donor regions are the country or region from which an invasive species or a particular genetically identified population originates
Ecosystem services:	The benefits that people receive from nature. More recently, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) introduced Nature's Benefits to People in 2015 (Díaz et al. 2015a, b)
Globalization:	The growing interdependence of the world's economies, cultures, and populations, brought about by cross-border trade in goods and services, technology, and flows of investment, people, and information (Peterson Institute for International Economics, piie.com)
Global governance:	Political cooperation among countries that aims to negotiate responses to shared challenges affecting more than one state or region
Global strategies:	Evidence-based policy agreements that coordinate multinational efforts to address patterns, mechanisms, and impacts of biological invasions
Invasive alien species:	Species, lower taxa, or genotypes introduced to an ecosystem where they are nonindigenous and likely to cause harm to biodiversity, the economy, public health, or the environment. However, there is no globally accepted definition of "harm," and often no generally accepted definition even within a single country
Phytosanitary:	Refers to the health of plants, especially with respect to the requirements of international trade
Recipient regions:	Recipient regions are the country, region, or ecosystem where the invader is introduced and established

and efficient in the use of limited budgets and resources, and more developed countries need to invest in supporting global action for the prevention of IAS.

Effective leadership to prevent and manage IAS is complicated by its multi-scalar distribution across geopolitical boundaries and the diverse political, economic, and cultural perspectives of stakeholders in donor and recipient regions that cause and suffer from biological invasions. The complexity and interconnectivity of biological invasions with culture, commerce, and political exigencies make their prevention and management particularly challenging. Invasions can directly affect humans by impacting health and socioeconomic systems (Bacher et al. 2018). To

prevent and reduce invasions, policies are needed at the international, national, and regional levels, yet most management actions (with some notable exceptions, examples of which are given below) necessarily occur at the local level, where custodianship, ownership, and governance to protect ecosystems may be the strongest. This disconnect makes coherent and enforceable policies across scales and jurisdictions complicated. Shifting governance and political trends also complicate designing and implementing global strategies. For example, some countries like the United States have recently taken steps backward in terms of national and coordinated international strategies in preventing and managing invasions (Meyerson et al. 2019). It is increasingly clear that effective

prevention and management of biological invasions requires a global governance approach, i.e., global-level leadership and coordination, which is prioritized by national governments from all countries with opportunities for different levels of buy-in depending on the capacities of the nation state.

The aim of this chapter is to highlight the need for global strategies to improve knowledge for the prediction, prevention, and management of IAS by coordinated efforts globally. While this book primarily focuses on plant invasions, the strategies discussed here apply not only to invasive plants but to all invasive taxa. We recognize that some specific strategies might need to be tailored to particular taxa. In a recent paper, Packer et al. (2017) advocated for global-scale research networks as an approach to address the intractable and large-scale questions related to biogeography that are fundamental to deepening our insights in invasion science. Here, we focus on policy and resulting management tools as a path toward effective coordinated strategies, including regulatory frameworks that combine incentive and compliance to address the increasing threats to biodiversity and ecosystem services posed by

invasive species. We review major existing global research, policy, and management approaches to invasions, describe existing networks that use global or multiscale tools to better address invasions, and outline essential elements for global strategies to improve prevention and management of biological invasions.

16.2 What Are Global Strategies?

Although the need for global approaches to manage biological invasions is well recognized in invasion science – and already featured in some international legislations – achieving effective global strategies remains elusive. Globally oriented networks (Table 16.1) exist for knowledge generation (e.g., Kueffer et al. 2014; Packer et al. 2017), knowledge management (e.g., database curation, Environmental Impact Classification for Alien Taxa (EICAT)/Socio-Economic Impact Classification for Alien Taxa (SEICAT) risk assessments), and voluntary engagement in global policy guidelines (e.g., ISSG, Tables 16.2 and 16.3). However, no binding global strategy for the management of IAS has previously been

Table 16.2 Existing intergovernmental and international organizations with an IAS focus

Acronym	Full name	Stated purpose	Temporal scale	URL
IPBES	Intergovernmental science-policy platform on biodiversity and ecosystem services	To strengthen science-policy interface for biodiversity and ecosystem services for the conservation and sustainable use of biodiversity, long-term human well-being, and sustainable development. From 2019 to 2023, IPBES is developing the global thematic assessment of invasive alien species and their control	8 years (2012–ongoing)	ipbes.net/
ISSG	IUCN invasive species specialist group-ISSG	Global network of scientific and policy experts on invasive species, organized under the auspices of the species survival commission (SSC) of the International Union for Conservation of nature (IUCN)	26 years (1994–ongoing)	issg.org/
OIE	World Organization for Animal Health	Intergovernmental organization responsible for improving animal health worldwide. The need to fight animal diseases at global level led to the creation of the Office International des Epizooties (OIE) through the international agreement signed on January 25, 1924. In 2003, the Office became the World Organization for Animal Health but kept its historical acronym OIE	96 years (1924–ongoing)	oie.int/

Table 16.3 Current international agreements related to invasive species prevention and management

Acronym	Convention/Treaty (if applicable)	Full name under convention or treaty	Description	Level of influence	No. of Parties
BWM	International convention for the control and Management of Ship's ballast water and sediments		Aims to prevent spread of harmful aquatic organisms from one region to another, by establishing standards and procedures for the management and control of ships' ballast water and sediments (2004) www.io.org/ www.imo.org/en/About/Conventions/ListOfConventions/Pages/International-Convention-for-the-Control-and-Management-of-Ships'-Ballast-Water-and-Sediments-(BWM).aspx	Legally binding (standard, record book, and certification)	8 signatory bodies and 81 contracting states
CBD	Convention on biological diversity	Article 8(h)	The CBD and its members recognize that there is an urgent need to address the impact of invasive alien species. Article 8(h) of the CBD states that "each contracting party shall, as far as possible and as appropriate, prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species." the CBD sets global priorities and guidelines, collects information, and helps to coordinate international action on invasive alien species The website also provides further information on invasive species and relevant decisions of the conference of the parties to the CBD www.cbd.int/convention/articles/default.shtml?a=cbd-08 www.fao.org/3/y5968e/y5968e0x.htm www.cbd.int/convention/articles/default.shtml?a=cbd-08	Legally binding	196
CBD	Convention on biological diversity	Aichi target 9	Aichi target 9 By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment www.cbd.int/sp/targets/rationale/target-9/		
CBD	Convention on biological diversity	Conference of parties (COP)	Alien species that threaten ecosystems, habitats, and species (CBD COP 6 Decision VII/23, April 2002) to which are annexed the Guiding Principles for the Prevention, Introduction and Mitigation of Impacts of Alien Species that threaten Ecosystems, Habitats or Species www.cbd.int/decision/cop/?id=7197 www.cbd.int/doc/decisions/cop-06-dec-23-en.pdf		
CITES	Convention on international trade in endangered species of wild Flora and Fauna		Multilateral treaty to protect endangered plants and animals. It was drafted as a result of a resolution adopted in 1963 at a meeting of members of the International Union for Conservation of nature. The convention was opened for signature in 1973 and CITES entered into force on July 1, 1975 cites.org/	Legally binding (licensing system)	183

CMS	Convention on migratory species of wild animals		Environmental treaty under the aegis of United Nations environment Programme, global platform for conservation and sustainable use of migratory animals and their habitats. CMS brings together the states through which migratory animals pass, the range states, and lays the legal foundation for internationally coordinated conservation measures throughout a migratory range. CMS is also known as the Bonn convention cms.int/	Legally-binding (framework)	128
IHR (2005)		International Health Regulations (1969)	The International Health Regulations (2005) are an international law which helps countries work together to save lives and livelihoods caused by the international spread of diseases and other health risks. They entered into force on June 15, 2007 and are binding on 194 countries across the globe, including all WHO Member States. The IHR (2005) aim to prevent, protect against, control, and respond to the international spread of disease while avoiding unnecessary interference with international traffic and trade. The IHR (2005) are also designed to reduce the risk of disease spread at international airports, ports, and ground crossings who.int/	Legally binding	Not stated
IPPC	International plant protection convention		The international plant protection convention (IPPC) is a legally binding treaty on plant health administered by the food and agriculture organization (FAO) but implemented through the cooperation of member governments and regional plant protection organizations. The goal of the IPPC is to coordinate work to prevent the spread and introduction of pests of plants and plant products and to promote appropriate measures for their control, with minimal disruption to trade. The IPPC develops international standards for phytosanitary measures (ISPMs) ippc.int/	Legally binding (framework)	183
Ramsar	Ramsar convention on wetlands of international importance especially as waterfowl habitat		An international treaty for the conservation and sustainable use of wetlands. It is also known as the convention on wetlands. It is named after the city of Ramsar in Iran, where the convention was signed in 1971 ramsar.org/	Legally binding	170

(continued)

Table 16.3 (continued)

Acronym	Convention/Treaty (if applicable)	Full name under convention or treaty	Description	Level of influence	No. of Parties
UNCLOS	United Nations convention on the law of the sea		An international treaty adopted and signed in 1982 and replacing the four Geneva Conventions of April, 1958, which respectively concerned the territorial sea and the contiguous zone, the continental shelf, the high seas, fishing, and conservation of living resources on the high seas. The Convention has created three new institutions: the International Tribunal for the Law of the Sea , the International Seabed Authority , and the Commission on the Limits of the Continental Shelf . The Convention has become the legal framework for marine and maritime activities, and IUCN and its partners are working toward an implementing agreement (UNCLOS IA) that will close important gaps in governance. A positive result would provide a measure of protection and conservation of Areas Beyond National Jurisdiction (ABNJ) where there is none at present www.un.org/Depts/los/convention_agreements/convention_overview_convention.htm?src=TREATY&mtdsg_no=XXI-6&chapter=21&Temp=mtdsg3&clang=_en	Legally binding	157
UN SDGs	The sustainable development goals report	15.8 prevent invasive alien species on land and water ecosystems	The 2030 Agenda for Sustainable Development was launched in 2015 to end poverty and set the world on a path of peace, prosperity, and opportunity for all on a healthy planet. The 17 Sustainable Development Goals (SDGs) demand nothing short of a transformation of the financial, economic, and political systems that govern societies today to guarantee the human rights of all. They require immense political will and ambitious action by all stakeholders unstats.un.org/sdgs/	Non-legally binding	193

UN watercourses convention	Convention on the law of non-navigational uses of international watercourses		International treaty, adopted by the United Nations in 1997, pertaining to the uses and conservation of all waters that cross international boundaries, including both surface and groundwater. The UN drafted the document to help conserve and manage water resources for present and future generations. From the time of its drafting, the convention took more than 17 years to enter into force on August 17, 2014, with the treaty having been ratified by just 36 states, the majority of countries remain outside its scope. The convention, however, is regarded as an important step in establishing international law governing water treaties.un.org treaties.un.org/Pages/ViewDetails.aspx?src=TREATY&mtdsg_no=XXVII-12&chapter=27&lang=en	Legally binding	39
WTO	The World Trade Organization	SPS agreement - agreement on the application of sanitary and phytosanitary measures	The WTO agreement on the application of sanitary and phytosanitary measures (SPS agreement). The agreement entered into force with the establishment of the World Trade Organization on January 1, 1995. It concerns the application of food safety and animal and plant health regulations. The SPS agreement is administered by the committee on sanitary and phytosanitary measures (the “SPS Committee”), in which all WTO members can participate wto.org/ www.wto.org/english/tratop_e/sps_e/spsund_e.htm	Encourages governments to establish own regulations based on international standards	Not stated

Note: International agreements may range from legally binding treaties (called Agreements) to less formal instruments, such as Memoranda of Understanding (<https://www.cms.int/en/legalinstrument/cms>)

proposed. International cooperation does exist for some circumstances where management can have international implications. For example, because introduced biological control organisms do not respect political boundaries, the Technical Advisory Group for Biological Control Agents of Weeds was formed in North America. This group advises the US Department of Agriculture Animal and Plant Health Inspection Service and has members from the United States, Canada, and Mexico (USDA APHIS, accessed 23 July 2020). However, such groups are the exception rather than the norm.

To illuminate the gap between the existing and recommended approaches, here we define the characteristics of global strategies within invasion science. While *global networks* focus on building evidenced-based knowledge and management, *global strategies* focus on evidence-based vision and policy, as well as management. Addressing the challenges of IAS requires globally integrated approaches to predict, prevent, and manage IAS, with considerations of the level of development and capacity of individual nations (Latombe et al. 2017). Therefore, an effective global strategy for biological invasions must be both locally relevant and identify the relationships between the global and local causes and impacts of IAS to economic, social, environmental, public health, and political outcomes. Below, we provide examples of past and extant global organizations and strategies (Table 16.2) that focus on IAS.

Building on the criteria for global networks (Packer et al. 2017), we define global strategies as frameworks for evidence-based visions, policy agreements, and commitments that coordinate multinational efforts to address the patterns, mechanisms, and impacts of biological invasions. Although advanced by global cooperation, the criteria for such strategies may be implemented at the global (e.g., requirements for treatment of ballast water along shipping routes, funding for data collection networks), as well as at continental or finer scales where they can be best addressed by multiple regions yet benefit all nation states (e.g., phytosanitary agreements). Therefore, a workable global strategy needs to be modular – i.e., must have components that countries can buy

into or not, depending on the availability of resources and political will. It is obvious that not all countries can or will opt for the comprehensive model with all recommended components, thus requiring a “hierarchy of strategies” model to maximize inclusion. Consequently, effective global strategies against biological invasions must include the following:

- (i) Address biological invasions at the global scale through a biogeographic lens of nation states.
- (ii) Consider legally binding regulatory frameworks, which may include optional self-regulatory or voluntary components, to address shared global priorities.
- (iii) Coordinate data management to ensure harmonization of data captured at different locations and of rigorous data analysis.
- (iv) Build, monitor, and maintain long-term collaborations and trust between member states and their representatives, including a shared understanding of an agreed, but realistic, action timeframe to target complex IAS dynamics.

16.2.1 A Brief Overview of Global Initiatives on Biological Invasions

Efforts to prevent and manage IAS have been developed at the global scale over the past 30 years (Foxcroft et al. 2017). In recognition of the growing number of species transported across geographic barriers and the related major risks and negative impacts, a global assessment of biological invasions was organized by the Scientific Committee on Problems of the Environment (SCOPE), a body of the International Council of Scientific Unions. This 3-year program attempted to draw some generalities by focusing on a number of key questions that invasion scientists still wrestle with today: (i) What are the characteristics of a successful invader? (ii) What characteristics determine the susceptibility to invasion? (iii) How successful are attempts to predict the outcome of an introduction? (iv) How should knowledge be used to manage invaded ecosystems?

The Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission (SSC) is a global network of science and policy experts on invasive species, organized under the auspices of the Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN). The ISSG was established in 1994 and currently has 196 core members from over 40 countries and a wide informal global network of over 2000 conservation practitioners and experts, who contribute to its work. The overall aim is to highlight and mainstream invasive species issues, such that they are addressed in an ecosystem context. Activities include providing technical and scientific advice to IUCN members in their work on invasive species, especially in international fora (e.g., Convention on Biological Diversity, CBD; the Ramsar Convention on Wetlands; International Maritime Organization, IMO), and work in the regions. The ISSG membership also provides technical and scientific advice to national and regional agencies in developing policies and strategies to manage the risk of biological invasions (Table 16.2).

The Global Invasive Species Programme (GISP) was initially developed in January 1996 and established in 1997 to address the global threats caused by IAS and to provide support to the implementation of Article 8(h) of the Convention on Biological Diversity. It was coordinated by the Scientific Committee on Problems of the Environment (SCOPE), in collaboration with the World Conservation Union (IUCN), and the Centre for Agriculture and Bioscience International (CABI). Participating groups and individuals made substantial in-kind contributions (McNeely et al. 2001). GISP contributed extensively to the knowledge and awareness of invasive species and developed a guide, *Invasive Alien Species: A Toolkit of Best Prevention and Management Practices*, to address the problem and a *Global Strategy on Invasive Alien Species* composed of ten strategic responses to address the problem of IAS (Box 16.2).

Most recently established, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) assesses the state of biodiversity and the ecosystem services provided to society in response to requests from decision-makers (Díaz et al. 2015a, Table 16.2). IPBES has

Box 16.2 Ten strategic responses recommended in the GISP 2001 *Global Strategy on Invasive Alien Species* (<http://www.issg.org/pdf/publications/GISP/Resources/McNeeley-et-al-EN.pdf>) along with the theme of the proposed strategy that it addresses most directly indicated in parentheses

1. Build management capacity (capacity).
2. Build research capacity (capacity).
3. Promote sharing of information (prevention).
4. Develop economic policies and tools (prevention).
5. Strengthen national, regional, and international legal and institutional frameworks (prevention and management).
6. Institute a system of environmental risk analysis (prevention).
7. Build public awareness and engagement (prevention).
8. Prepare national strategies and plans (management).
9. Build invasive alien species issues into global change initiatives (management).
10. Promote international cooperation (capacity).

defined five major drivers of biodiversity decline at a global scale: land-use change, direct use, pollution, climate change, and invasive species (Brondizio et al. 2019). For invasive species, since 2019, IPBES is carrying out a thematic global assessment with the specific objective, “To assess the threat that invasive alien species pose to biodiversity, ecosystem services and livelihoods and the global status of and trends in impacts of invasive alien species by region and sub-region, taking into account various knowledge and value systems” (IPBES 2018). With 87 experts from 46 countries, as of August 2020, this assessment is anticipated to bring together the latest comprehensive state-of-the-art knowledge on invasive species and the strategies to control them at local and global scales and

is expected to be approved by the intergovernmental plenary at the Plenary's tenth session (IPBES-10), in May 2023. A key element of this assessment is that all evidence should be informative for global and national policy-making. Therefore, the assessment considers not only biological evidence but also economic and social aspects that are critical for building effective conservation strategies.

These global initiatives are complemented with numerous regional, national, and thematic approaches (e.g., related to particular biomes, organism groups, or introduction pathways, McDougall et al. 2011; Wilson et al. 2011; Brunel et al. 2013) and voluntary approaches (discussed in the following paragraph). For example, in South Africa, there is a high level of awareness on issues related to invasions, and the recently approved strategy to manage biological invasions is supported by national legislation and government-level funding. South Africa has adopted a diversified approach to managing invasive species, including employment creation and ecological restoration. While recognizing that eradication is not feasible for most invasive species, South Africa seeks to minimize the impacts of invaders at the lowest possible cost and in as many locations as possible in perpetuity (van Wilgen 2018).

A mix of legally binding and voluntary approaches is highly likely to produce the most effective global strategies for the prevention and management of IAS. Therefore, equally important to successful global strategies are voluntary "codes of conduct," standards, and certification schemes (such as for forests), which set practices to prevent, restrict, or exclude the use of IAS. For example, Brundu and Richardson (2016) and Brundu et al. (2020) proposed a voluntary code of conduct and global guidelines for planted forest and non-native trees which complement similar codes for planted forest, botanical gardens, and ornamental horticulture. The code for planted forests is comprised of 14 principles and is relevant to all stakeholders and decision-makers in the 47 member states in the Council of Europe (Brundu and Richardson 2016). Forest certification standards, such as those of the Forest Stewardship Council (<https://fsc.org/en>) and PEFC (Programme for the Endorsement of Forest Certification schemes), regulate the use of alien trees to prevent invasions

outside of plantations by straddling voluntary and legally binding approaches. Another relevant example is ISPM 41 (FAO 2017), i.e., the International Standard for Phytosanitary Measures which identifies and categorizes the risk associated with the international movement of used vehicles, machinery, and equipment utilized in agriculture, forestry, horticulture, earth moving, surface mining, waste management, and the military. The standards identify appropriate phytosanitary measures to reduce the accidental spread of pests, including invasive alien species.

In addition to global strategies, disciplinary or thematic research networks have changed the ways in which we understand and address invasions, including the invasibility of specific ecosystem types (e.g., Mountain Invasion Research Network, Alexander et al. 2016, International Council for the Exploration of the Sea), deepening our understanding of the impacts resulting from invasions (e.g., Environmental Impact Classification of Alien Taxa, Hawkins et al. 2015), and curated data that enables these assessments (e.g., DAISIE, Hulme et al. 2009; GloNAF, Pyšek et al. 2017; van Kleunen et al. 2019). Complementing these knowledge networks are policy-oriented collaborations (e.g., IUCN, ISSG) that provide guidance for regional (e.g., European Union) and state (e.g., Australia) mechanisms to address the risks associated with the introduction of alien species (e.g., as pets, live bait, food, or unintended stowaways (UNEP 2016) and impacts where alien species establish and become invasive. Despite the concerted efforts of many networks and important progress on developing evidence-based policy, current knowledge and policy have failed to halt the escalating spread and impact of invasive organisms. More effective coordination and interventions (e.g., Waage and Reaser 2001; Kumschick et al. 2017) that require less reliance on voluntary goodwill and a more mandated systemic and legislative approach (Banks et al. 2015) are needed. The greatest challenges are identifying and negotiating the remaining knowledge, policy, and drivers (e.g., incentives) to increase proactive prevention that benefits all states and to achieve binding strategies where appropriate, or voluntary actions.

16.2.2 Key Elements of Global Strategies and Main Planning Tools

The science and techniques of strategic planning have an extensive history that includes multiple and competing theories to explain the strategic planning process and its relationship to formulating and achieving management objectives (Papke-Shields and Boyer-Wright 2017). In this section, we review some of the key elements for successful strategies, including strategic planning, scenario planning, strategic management, and execution of global strategies for better prevention and management of IAS, with a special focus on the application of these elements in the field of invasion science.

Strategic planning has a visionary component, but care must be exercised to ensure that all objectives are specific, measurable, action-oriented, realistic, and time-bound (SMART, McDermott et al. 1999). For example, the vision statement of the Australia Weed Strategy 2017–2027 aims to “Protect Australia’s economic, environmental and social assets from the impacts of weeds.” A strengths, weaknesses, opportunities, and threats (SWOT) analysis, or SWOT matrix, is a model used at the beginning of an organization’s strategic planning. Strengths and weaknesses are considered internal factors, while opportunities and threats are considered external factors. Genovesi et al. (2010) identified five distinct options for a European Early Warning and Rapid Response (EWRR) system (i.e., voluntary network of national authorities, non-institutional panel, inter-governmental coordinating body, intergovernmental agency, intergovernmental central authority). In their report, a concise description of the organizational model for each of the options was presented, along with a SWOT analysis to facilitate evaluation of the alternatives. At a local scale, Mukwada and Manatsa (2017) carried out a SWOT analysis of the policy framework guiding the control of the invasion of the Australian tree *Acacia mearnsii* and other IAS in the Golden Gate Highlands National Park in South Africa. The implementation of restoration measures in the park and adjacent communities was in line with the recommendations of the Convention on

Biodiversity. They identified the need to strengthen relationships with the community in the park, improve legislation, and boost the technical capacity of parks in South Africa to manage IAS. Following such an analysis, a *strategy map* is a useful tool for strategic planning, especially at the global level. A strategy map is a visual tool designed to clearly communicate a strategic plan and achieve the desired goals. Strategy mapping should be a major part of any strategic document that offers an excellent way to communicate the knowledge across the committed organization(s) and the stakeholders in an easy-to-follow format.

Scenario planning is a management tool that originated in the trade and business world that enables executives to develop strategies in uncertain business environments (Oliver and Parrett 2018). More recently, this tool has been applied by Yemshanov et al. (2017) to the invasion of the Asian long-horned beetle (*Anoplophora glabripennis*) in Ontario, Canada. They proposed a scenario optimization model that incorporates uncertainty about the spread of an invasive species and allocates survey and eradication measures to minimize the number of infested, or potentially infested, host plants on the landscape. Booy et al. (2020) assessed the possibility of eradicating dozens of established but not yet invasive species in the EU and found that eradication feasibility and risk scores were not correlated, suggesting each approach uses distinct criteria. Using a horizon scan, they further identified more than two dozen new species that are priorities for immediate or high-priority eradication.

Strategy review and refinement is necessary to ensure that the right course of action is being taken. For example, the Phytosanitary Capacity Evaluation (PCE) is a diagnostic tool enabling countries to assess the weaknesses and strengths of phytosanitary systems in relation to their ability to fully implement the International Plant Protection Convention (IPPC, Table 16.3) and other international phytosanitary obligations and standards. The PCE has also been applied as a cross-disciplinary tool among the sanitary, phytosanitary, and food safety areas in the Andean subregion in South America. Since IAS are often a significant subset of “quarantine pests,” as defined

by the IPCC, PCE results are already useful in relation to invasive species. The PCE methodology has the potential to be further developed to cover a country's needs in implementing Article 8(h) of the Convention on Biological Diversity (CBD, Table 16.3, discussed below in Sect. 16.2.3). Through its integration at the global scale with existing international IAS and mountain networks such as the Global Mountain Biodiversity Assessment (GMBA) and Mountain Research Initiative (MRI), the CBD reaches out to the broader research and management communities. This approach has helped to improve management strategies specific to mountains (Kueffer et al. 2013a), enlarged the databases on alien and invasive plants at high elevations, and furthered the understanding of the specific processes driving plant invasions in mountains (Kueffer et al. 2013a). The example of mountain invasions (Box 16.3) that were long neglected in the global science and

Box 16.3 The Mountain Invasion Research Network (MIREN)

The Mountain Invasion Research Network (MIREN, www.mountaininvasions.org) has over 15 years of experience in bringing together academic and nonacademic expert groups (invasion and mountain scientists, managers) to understand biological invasion processes and support management actions to prevent and control IAS in mountains. The scientific aim of MIREN is to understand the effects of global change on species' distributions and biodiversity in mountainous areas. While the initial focus was on non-native plant invasions, it now considers more generally species redistribution along elevational gradients under different drivers of global change, including climate and land-use change. The network uses observational and experimental studies along elevation gradients across multiple sites at all latitudes worldwide to evaluate and quantify the processes and mechanisms that are shaping mountain

plant communities at regional to global scales. MIREN includes over 20 sites on all continents, except Antarctica. Its taxonomic focus has been mainly in plants, but its experience is useful for any taxa.

Four elements of the MIREN approach can be useful for designing similar networks focused on other invasions (e.g., in particular habitat types, for specific taxonomic groups, or in association with certain invasion pathways such as horticulture or forestry), (adapted from Kueffer et al. 2014):

1. **Global network with local support:** MIREN is a multiscale network that links local scales with the global scale by integrating a global network of local case studies into existing international invasive species and mountain networks. A bottom-up structure with two elected co-chairs from different case study regions has helped to maintain the network dynamics.
2. **Inter- and transdisciplinary work:** MIREN links two interdisciplinary fields of expertise on invasive species and mountains with local practitioners and stakeholders.
3. **Non-centralized funding:** MIREN has never been centrally funded by one large grant; rather, it is the collective effort of local grants that support the networks' activities. This increases flexibility and long-term sustainability that are often lacking in the case of single-grant funding.
4. **Adaptive research:** The observational and experimental research that MIREN uses across all sites is tightly linked to the experience of local managers. The scientific goals and methods are discussed across academic and nonacademic MIREN members from all regions. This ensures that research approaches can be regularly adapted to emerging management needs or new scientific questions in the different world regions.

management community shows how important it is to tailor global strategies to particular ecological contexts (such as mountain environments) and ensure a bottom-up process (Kueffer et al. 2013b).

Strategic management is usually defined as the comprehensive collection of ongoing activities and processes that organizations use to systematically coordinate and align resources and actions with mission, vision, and strategy (Strickland and Thompson 1995; Pressey et al. 2013). Strategic management activities transform the static strategic plan into a system that provides strategic performance feedback to decision-making and enables the plan to evolve and grow as requirements and circumstances change.

Strategy execution is basically synonymous with strategy management and amounts to the systematic implementation of a plan of action. Both the “planning” or rational method and the “learning” or adaptive method could be applied to strategy drafting and strategic management for IAS. In practice, however, the demarcation between planning and learning approaches has become more and more blurred, and a major problem in IAS management is uncertainty (Latombe et al. 2017; Robertson et al. 2020). Managers can be faced with at least four (Latombe et al. 2019) main types of uncertainty: (1) to clearly circumscribe the invasion phenomenon, (2) to measure and provide evidence for the phenomenon (i.e., confirmation), (3) to understand the mechanisms that enable the phenomenon, and (4) to understand the mechanisms through which the phenomenon results in consequences. Active adaptive management (AAM) is a deliberate plan for learning about the managed system, which can be improved in the face of uncertainty. For example, the potential benefits of applying AAM has been identified for insect pest and weed control (Shea et al. 2002).

A key stage in strategy building is engagement with actors to achieve ownership of strategies, a supportive institutional framework, and the ability to continuously learn and adapt (Novoa et al. 2018; Shackleton et al. 2019a). Given the hybrid local and global nature of the invasive species phenomenon, strategies must be locally rooted but globally connected. The Mountain Invasion Research

Network (MIREN, Table 16.1) is an example of a global invasive species network that enables a transdisciplinary, multiscale learning process at the science-policy interface (Kueffer et al. 2013a). MIREN encompasses about 20 case study sites carefully selected from different ecological (subarctic to tropical, continents, and islands) and socioeconomic contexts (developing and developed countries), including both research and management institutions at the sites (Box 16.3). It aims to strengthen anticipatory research and precautionary management through replicated local case studies and cross-site learning; in other words, it creates globally distributed local communities of practice. In summary, “MIREN has established a ‘community of practice,’ including experts from both academia and management institutions, that is global but locally-rooted and capable of addressing diverse multi-scale global change problems in mountains” (Kueffer et al. 2014).

16.2.3 Existing Legislation Supportive of Invasive Species Global Strategies and International Cooperation

A myriad of organizations, with diverse mandates and residing in a wide range of government departments, support global strategies on invasive species prevention and management (Table 16.3). For example, since 1992, the Convention on Biological Diversity (CBD 1993) has identified IAS as a major cross-cutting theme. This global treaty requires Parties “*as far as possible and as appropriate, (to) prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species*” [Article 8(h)]. In 2002, the CBD Conference of the Parties (COP) adopted specific decision and guiding principles to help parties implement this policy instrument. The 2002 decision urges parties, other governments, and relevant organizations to prioritize the development of IAS strategies and action plans at national and regional level and to promote and implement the CBD Guiding Principles.

In addition to the CBD, the SPS (Sanitary and Phytosanitary Measures) Agreement, standards of the IPPC and OIE (World Organization for Animal Health, formerly the Office International des Epizooties), and several other international regulations and conventions – particularly the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES), the International Ballast Water Management Convention, the Bern Convention, the Ramsar Convention, and the International Health Regulations – are relevant for different aspects of IAS and represent an important legal foundation for any global strategy on biological invasions. Similarly, a large number of international and nonprofit organizations are involved in efforts focused on raising awareness, prevention, monitoring, control, and/or eradication of invasive species, including capacity building and strategic planning or management. Several nations have developed recommendations or guidance on pest and animal movements related to invasions. While some of this work is binding on countries, much is voluntary or can be classified in the more general category of “soft law.” The number of conventions and organizations that are relevant to prevention, control, and eradication underpins both the importance and challenge of ensuring synergies and coherence in order to avoid overlaps and gaps. In fact, the Inter-Agency Liaison Group on Invasive Alien Species was established to facilitate such cooperation (www.cbd.int/invasive). Besides the need for effective interagency and interdisciplinary cooperation at the global level, collaboration is essential among national authorities responsible for different aspects of IAS (WTO 2013).

Measures to prevent the introduction or limit the spread of IAS may, by their nature, be trade restrictive. Close alignment between the CBD and the WTO SPS Agreement, as well as among other relevant international organizations, is therefore beneficial to help achieve the objectives of these instruments without restricting trade (Lopian 2005). The relationship between international trade and IAS was the focus of a seminar organized by the Standards and Trade Development Facility (STDF), in collaboration

with the IPPC, the OIE, and the WTO, in July 2012. The seminar was successful in raising awareness about the mutually beneficial goals of the CBD and the SPS Agreement and the contribution of the two relevant standard-setting organizations (IPPC, OIE) under the SPS Agreement (WTO 2013).

16.3 Responding to Novel Threats: Further Developing Global Networks and Knowledge Systems to Support Global Strategies

Newly emerging opportunities for the introduction of organisms to the non-native regions, associated with the opening of new pathways (Hughes et al. 2020), require improved knowledge systems and tools that would allow dealing with these fresh invasions. In this section, we present examples of such new pathways (emerging trade, including e-commerce, and increasing travel routes) and describe approaches (common garden experiments) and tools (databases) for improving our knowledge base (focused research involving novel species, novel technologies, and tools) that can be used to design novel strategies on IAS.

16.3.1 Global Data Registries, Data Harmonization, and Standardization

Resourcing and rewarding global registries for data collection and research on invasions are avenues to support global strategies that focus on policy and management. Nations could manage global coordination through memoranda of understanding (MOUs). Table 16.4 provides examples and descriptions of databases and data repositories that cover large spatial scales (in some cases, global) that have advanced invasion research, management, and policy. Nonetheless, significant gaps in geographic, pathways’ relationship, and taxonomic coverage persist. Increasingly, databases are paying attention to biases and gaps in the distribution of data. Data gathering efforts

Table 16.4 Examples of databases and repositories that focus on invasive species or include data relevant to biological invasions

Acronym	Full name	Description	URL
Alien floras and faunas	Series in the journal <i>Biological Invasions</i> on alien floras and faunas	Alien floras and faunas includes papers and data that provide information on complete alien floras or faunas of large regions, such as countries, with clearly described criteria used to assess the species' status as casual, naturalized, or invasive. Full species lists with relevant available information must be published with the paper as electronic supplementary material	Pyšek et al. (2018)
BISON	Biodiversity information serving our nation	Web-based federal mapping resource for species occurrence data in the United States and its territories. Researchers collect species occurrence data, records of an organism at a particular time in a particular place	bison.usgs.gov/#home
CABI	CABI invasive species compendium	The invasive species compendium (ISC) is an encyclopedic resource that brings together a wide range of different types of science-based information to support decision-making in invasive species management worldwide. The US Department of Agriculture is a lead partner with CABI in the development of this compendium which has been resourced by a diverse international consortium of government departments, non-governmental organizations, and private companies. The horizon scanning tool is a decision support aid that helps you identify and categorize species that might enter a particular geographic area from another geographic area	www.cabi.org/ISC www.cabi.org/horizonscanningtool
DAISIE	Delivering alien invasive species inventories for Europe	A structured inventory of invasive species that threatens European terrestrial, freshwater, and marine environments to provide the basis for prevention and control, to assess and summarize the ecological, economic, and health risks and impacts for early warning	www.europe-alien.org/
EPPO GDB	European and Mediterranean Plant Protection Organization Global Data Base	The EPPO global database is maintained by the secretariat of the European and Mediterranean Plant Protection Organization. The aim of the database is to provide all pest-specific information that has been produced or collected by EPPO. The database contents are constantly being updated by the EPPO secretariat. It holds basic information for more than 88,000 species of interest to agriculture, forestry, and plant protection	gd.eppo.int/
GLONAF	Global naturalized alien Flora	A living database on alien plants that is both research and policy relevant	van Kleunen et al. (2019)
GLOPNET	Global plant trait network	A research collaborative that studies and compiles data on plant traits in order to synthesize existing data to answer new questions and encourage further study on plant traits	bio.mq.edu.au/~i.wright/gloplan.htm

(continued)

Table 16.4 (continued)

Acronym	Full name	Description	URL
GRIIS	Global register of introduced and invasive species	The global register of introduced and invasive species provides country-wise checklists of introduced and invasive species. GRIIS was conceived to provide a sustainable platform for information delivery to support national governments. In the future, it aims to enable a global system for sustainable monitoring of trends in biological invasions that affect the environment	Pagad et al. (2018); https://doi.org/10.1038/sdata.2017.202
iNaturalist		One of the world's most popular nature apps, which helps to identify and map plants and animals, and to get connected with a community of over a million scientists and naturalists.	Spear et al. (2017); https://doi.org/10.33389/fevo.2017.00086
INVASIVESNET	International Association for Open Knowledge on invasive alien species	This association facilitates greater understanding and improved management of IAS and biological invasions globally by developing a sustainable network of networks for effective knowledge exchange	www.invasivesnet.org/
Kew genome size database	Plant DNA C-values database	The plant DNA C-values database currently contains C-value data for 12,273 species	cvalues.science.kew.org/
PREDICTS		As of August 2020, the PREDICTS database has >3.6 million biodiversity records from over 32,000 sites, covering more than 50,000 species. Database could be used to answer questions such as "Do changes in land-use facilitate success of invasive species?."	www.predicts.org.uk Hudson et al. (2016); https://doi.org/10.1002/ecc3.2579
TRY	Plant trait database	A global database of curated plant traits	www.try-db.org/de/Datasets.php

across geographic regions and taxonomic groups are key to addressing the problems invasive species pose (e.g., van Kleunen et al. 2015), and including new datasets, e.g., including iNaturalist data in IAS assessments, could be fruitful.

Bigger datasets could result in higher bias, so careful selection of data and appropriate statistical design should be ensured in order to limit correlated errors when handling big datasets (Deriu et al. 2017; Groom et al. 2017; Wang et al. 2018). Reducing barriers to data sharing and interoperability will significantly improve our ability to respond as quickly as possible to the challenges of biological invasions as trading partners and trade pathways shift and as global change brings new invasive species challenges to the fore.

16.3.2 Model Species

One way in which researchers have sought to better understand invasions and to gain insights for improved predictions is by adopting a model approach with a single species. Model organisms are a limited suite of species used to understand generalities among a larger group of organisms and can save time and resources in research. Kueffer et al. (2013b) suggested that model systems could help address “wicked” (*sensu* Woodford et al. 2016) questions in invasion science, including those at the global scale. Research that employs an appropriate model organism may help to identify mechanisms and processes underlying invasions and allow researchers to more rapidly test hypotheses and advance empirical invasion science. Developing model systems in invasion science is increasingly possible due to recent curation of comprehensive datasets (Table 16.4) and formation of both public and private collaborative research consortia (Table 16.1). Examples of model species in invasion science include the cosmopolitan grass *Phragmites australis* (Meyerson et al. 2016), the lady bird beetle *Harmonia axyridis* (Roy and Wajnberg 2008), and many others (e.g., Kueffer et al. 2013b; Novoa et al. 2020). The identification of appropriate model species in invasion science with open-access data registries not only could catapult research globally but also serves as a powerful tool for policy development, where model

species provide both cautionary tales and lessons learned for prevention and management.

16.3.3 Technologies and Tools to Develop Successful Global Strategies

Inexpensive and transferrable technologies – both low and high end – that can be easily shared and used around the world are needed to support global strategies to prevent and manage invasive species. For example, prior to import, relatively inexpensive diagnostic technologies such as flow cytometry can be used to quickly assess plant ploidy level and genome size – both correlates of plant invasiveness (te Beest et al. 2012; Pandit et al. 2014; Suda et al. 2015). Global citizen science platforms like iNaturalist (<https://www.inaturalist.org/>; Spear et al. 2017), and groups like the Conservation X lab (conservationx.com/challenge/invasives/zero), are challenging and inspiring people to ideate and develop innovative solutions to existing roadblocks in invasive species detection. People all over the world are stepping up to meet this challenge through the development of technologies like smartphone apps or identifying low-tech ways to solve “wicked problems.” Table 16.5 summarizes some of the technologies that are currently being used or are at developmental stage to manage IAS globally. As old technologies advance and newer ones emerge globally, and as cross-disciplinary collaborations grow, possibilities exist for their applications and the development of novel tools for global IAS strategies.

16.4 Concluding Remarks

While IAS challenges are global, the nature and severity of their impacts on biodiversity, economies, health, and society are unevenly distributed across nations and regions. Thus, some aspects of the problem require local or regional solutions tailored to the specific values, needs, and priorities of states or regions (e.g., islands, protected areas, local authorities, indigenous communities), while others call for consolidated action by the larger global community. Certainly, any global strategy

Table 16.5 Examples of available and readily transferable technologies that can be used to manage invaders in multiple regions or countries. The policies associated with the use of these technologies could be negotiated through shared governance processes

Technology	Description	Examples and applications	References
eDNA	Environmental DNA (eDNA) is the genetic material from a plant or animal that is found in the air, water, or soil or other substrata. It has recently emerged as a powerful genetic tool for detecting invasive species and rare aquatic organisms. This technology involves detection of DNA in an environmental sample, such as lake or river water	Fish, such as Asian carp, release DNA into the environment in the form of skin cells, secretions, and feces. This DNA can be collected from water samples in the field and be used to indicate the potential presence of an individual species. Zaiko et al. (2018) review the merits and limitations of this technology	Asiancarp.U.s/eDNA.Html Egan et al. (2013); https://doi.org/10.1111/conl.12017 Zaiko et al. (2018); https://doi.org/10.3389/fmars.2018.00322 Ruppert et al. (2019); https://doi.org/10.1016/j.gecco.2019.e00547 isac_advanced_biotechnology_white_paper.pdf Vasilidou et al. (2016); https://doi.org/10.1373/clinchem.2016.263186 Wang et al. (2016); https://doi.org/10.1146/annurev-biochem-060815-014607
Genome editing	Technique to insert, delete, or modify DNA to silence or activate specific genetic characteristics. The development of clustered regularly interspaced short palindromic repeats (CRISPR) combined with the Cas9 enzyme (CRISPR/Cas9) rapidly increased the specificity and efficiency of gene editing and decreased costs	Genome editing is currently being applied to human health and crop protection (e.g., vector-borne disease, crop pests). Potential future uses include invertebrate pests for sterile insect technique releases to cause mosquito eradication in Hawaii to eliminate avian malaria that is driving and inducing native species to be resistant to disease (e.g., bats for white-nose syndrome, amphibians for the fungal disease chytridiomycosis)	(NISC) isac_advanced_biotechnology_white_paper.pdf
Gene drives	Gene drives advance genome editing by introducing a mechanism that promotes the inheritance of a particular gene to increase its frequency in a population. The process “drives” the desired genetic trait through subsequent generations of offspring from the modified individual(s). Gene drives provide the potential to modify sexually reproducing wild populations by design	Gene drives allow specific genes to be inserted, modified, or deleted. They can be used to modify populations to no longer carry a disease or to alter the sex ratio of all offspring to all male. To date, CRISPR gene drives have been synthesized in yeast, fruit flies, and two species of mosquito (NAS 2016). Specific applications include mosquito control to limit the transmission of malaria and other vector-borne diseases, as well as possible use to eradicate invasive rodents on islands	
GIS	Geographic information systems are tools that allow users to create interactive queries, analyze spatial information, edit data in maps, and present the results of all these operations	In combination with remotely sensed data and geospatial data collected via field work or from existing available data, GIS can be used to map and analyze invasive species establishment and spread and relate environmental characteristics and anthropogenic effects to different invasion stages	Haluch et al. (2000); https://doi.org/10.4319/lo.2000.45.8.1778

(continued)

Table 16.5 (continued)

Technology	Description	Examples and applications	References
Horizon scanning	Horizon scanning is defined as a systematic examination of potential threats and opportunities within a given context. Horizon scanning to prioritize the threat posed by potentially new IAS which are not yet established within a region is seen as an essential component of IAS management	The horizon scanning techniques has been applied in the European Union, in the United Kingdom, and in other countries and regions. Lists of species are usually generated by individual experts and collated within thematic groups in advance of the workshop. Scores for risk criteria, coupled with information on the level of confidence of the relevant scores, are applied to species and reviewed to allow collation into one consensus list for each thematic group. An expert workshop is subsequently used to build consensus to derive a single agreed list of priority species across all thematic groups while also reviewing the process that produced the lists	Roy et al. (2014); https://doi.org/10.1111/gcb.12603
Novel poisons	Delivery of nontraditional toxicant to control an invasive species	Acetaminophen hidden in mice that are air dropped into Guam. The snakes ingest the poisoned mice and die	nationalgeographic.com/news/2010/09/100924-science-animals-guam-brown-tree-snakes-mouse-tylenol/
Remote sensing	Remote sensing is the process of detecting and monitoring the physical characteristics of an area by measuring its reflected and emitted radiation at a distance	Using remote sensing technology, existing populations of invasive species can be identified (classified) and mapped using GIS LiDAR (light detection and ranging) in the form of a pulsed laser used to measure ranges (variable distances) to the earth is a particular kind of remote sensing. In Yellowstone National Park, USA, it can be used to locate and capture non-native fish during the brief weeks each year when they come into shallow water to spawn Google earth engine is a freeware available to download and process freely available satellite imagery	(USGS) pubs.usgs.gov/fs/2011/3109/FS11-3109.pdf Roddewig et al. (2018); https://earthengine.google.com/

RNAi	Ribonucleic acid interference (RNAi) “silences” targeted genes. By the introduction of double-stranded RNA into the cell, it destroys the single-stranded messenger RNA with the same sequence	Can be used to provide resistance to pests and diseases and eliminate production of specific hormones or can be a taxa-specific toxicant. Future uses for invasive species control could include taxa-specific hormone suppressants in baits that would disrupt social dynamics or turn workers against queens, leading to colony collapse in invasive social invertebrates like ants	<p>Fire et al. (1998); https://doi.org/10.1038/35888</p> <p>Heath et al. (2014); https://doi.org/10.1371/journal.pone.0088387</p> <p>Owens and Malham (2015); https://doi.org/10.3390/jmse3010087</p> <p>Saleh et al. (2016); https://doi.org/10.1089/nat.2016.0613</p> <p>Huvenne and Smagge (2010); https://doi.org/10.1016/j.jinsphys.2009.10.004</p> <p>Xue et al. (2012); https://doi.org/10.1016/B978-0-12-387680-5.00003-3; isac_advanced_biotechnology_white_paper.pdf</p> <p>voanews.com/a/3824381.html</p>
Robotics	Remotely controlled robots to hunt invaders	Invasive lionfish hunted by autonomous underwater robots (e.g., Guardian LFI).	<p>apps.bugwood.org/apps/easin.jrc.ec.europa.eu/easin/CitizenScience/BecomeACitizen</p>
Smartphone technologies	Apps to rapidly identify and report invasives	<p>“Squeal on pigs” – Provide landowners with the information they need to effectively and quickly report suspected sightings of feral pigs and provide states with tools to work with private landowners to eradicate known populations of feral pigs</p> <p>“Texas invaders” – Citizen science program collects species observations from volunteer “citizen scientists” trained to use a specially developed invasive species Early detection and reporting kit</p>	<p>www.cbp.gov/FY2016AgricultureFactSheetUpdate_OFO.pdf; www.nature.com/articles/s41598-019-52385-1;</p> <p>Goodwin et al. (2010); https://doi.org/10.1614/IPSMS-D-09-00025.1</p>
Sniffer dogs (molecular dogs)	Trained canines that can detect plants and animals, diseases, etc.	The “beagle brigade” consists of beagles trained by the US Department of Agriculture to detect invasive species at airports and borders. They serve as assistants to their human inspectors	<p>www.cbp.gov/FY2016AgricultureFactSheetUpdate_OFO.pdf; www.nature.com/articles/s41598-019-52385-1;</p> <p>Goodwin et al. (2010); https://doi.org/10.1614/IPSMS-D-09-00025.1</p>

that hinders local action or makes IAS management more difficult at the local scale will be undesirable. An effective global strategy will facilitate nations to adopt parts of the strategy, or all of it, depending on their capacity and goals.

Building on the foundations of the GISP 2001 *Global Strategy on Invasive Alien Species* (Box 16.2), a five-point formulation is recommended to improve international capacity, prevention, and management of IAS through a global strategy:

1. **Better tools, indicators, and standards for long-term monitoring of biological invasions and management success at multiple scales.** Without a clear assessment of the magnitude and dynamics of biological invasions, it is impossible to establish a successful global strategy for their control. Thus, key indicators need to be established at multiple scales, from local to global scales. Countries should be required to make knowledge available about such indicators, and clear monitoring schemes ought to be implemented and followed consistently over time.
2. **Better techniques for the evaluation of impacts across different taxa and regions.** Quantitative estimations of the impacts of IAS on biodiversity, ecosystem services, and human well-being should be evaluated, and their results effectively communicated to all societies that are or may be affected. Likewise, national strategies should identify *agreed-upon management options* for controversial species (e.g., those producing both negative and positive impacts, e.g., see Pejchar and Mooney 2009; Kiviat 2013; Shackleton et al. 2014) and identify who should bear the costs of the negative impacts, as well as the costs and benefits of any control strategy. Equally important would be to weigh the gains and losses from such controversial taxa. Any assessment should also include the socioeconomic aspects (Bacher et al. 2018) and better techniques for communication, outreach, and citizen science that take into account different world views and values (Humair et al. 2014; Shackleton et al. 2019b) and enable collaboration with practitioners such as in the pet, aquarium, and plant trade industries (Hulme et al. 2018; Shackleton et al. 2019b).
3. **Better and additional legislation and normative tools (from global to local contexts).** Preventing the introduction and spread of IAS requires strict regulations that may in some cases be considered adverse for some stakeholders. Thus, unless these regulations are supported by national legislations, it will be impossible to advance them based only on the recommendations or voluntary approaches or just by the broad global agreements. Efforts must be directed to translate global initiatives into instrumental local regulations (e.g., Perrings et al. 2010). For example, while there is a convention on ballast water slowly taking effect, and although managers and policymakers have recently come to recognize the importance of biofouling of commercial vessels and recreational boats in the dispersal of IAS, no international convention exists to address this issue (Galil et al. 2015). In addition, better and more effective regulations in the trade of pets and ornamental plants are certainly required (Patoka et al. 2018).
4. **Better global biosecurity and biosecurity awareness.** Hulme (2014) defines biosecurity as “the research, procedures and policies that cover the exclusion, eradication or effective management of the risks posed by the introduction of alien plant pests, animal pests and diseases, animal diseases capable of transmission to humans (zoonoses) – Covid-19, the current pandemic is a prime example (Nuñez et al. 2020) – the introduction and release of genetically modified organisms (GMOs) and their products, and the introduction and management of IAS and genotypes.” This comprehensive definition incorporates patterns of trade and transport that facilitate species introductions (Meyerson and Mooney 2007). Nations such as Australia, New Zealand, and South Africa have invested heavily in biosecurity measures that include IAS as major biosecurity risks, while other countries like the United States have not heeded calls to include IAS as a significant biosecurity threat (Meyerson and Reaser 2002a, b; Meyerson

et al. 2019). Trade volume and international passenger travel have risen dramatically over the last several decades along with international trade agreements (Hulme 2014), all of which increase the risks of species introductions and overwhelm biosecurity efforts of many nations. Coupled with climate change and overall global human population growth, addressing biosecurity to include IAS adequately will require a global strategy. An approach known as the “biosecurity continuum” is a promising global strategy to raise awareness and reduce risks associated with the global movement of species. The biosecurity continuum efforts address the risks of IAS in three stages: (i) pre-border, to lower the risks posed by introductions from other countries; (ii) at the border, to stop IAS from entering a region; and (iii) post-border, to find and eradicate any IAS that were able to enter and establish (Caffrey et al. 2014; Hulme 2014). While implementing a biosecurity continuum on a global scale would present significant challenges, it could also provide substantial benefits to countries by demonstrating that their exports are IAS-free, thereby strengthening relationships among trading partners.

5. Increase synergies with other strategies on biodiversity and environmental protection.

A significantly large percentage of the world’s plant species, perhaps as many as 94,000–194,000, are at risk of extinction in the near future due to threats including habitat loss or degradation, overexploitation, biological invasions, industrialization, pollution, and climate change (Pitman and Jørgensen 2002; Brondizio et al. 2019). Efforts to conserve plant biodiversity are hindered by several factors, in particular by the lack of a comprehensive global inventory of plant species and insufficient data for assessment of the conservation status of each species (Miller et al. 2012). The Global Strategy for Plant Conservation (GSPC) was adopted in 2002 at the sixth meeting of the Conference of the Parties to the Convention on Biological Diversity at The Hague in the Netherlands to address these challenges, and it is a clear example of one strategy that could

work synergistically with a global strategy on biological invasions, producing overarching mutual benefits. Databasing plant diversity and promoting Red List assessments are of course very important not only for plant conservation but also to evaluate the impacts of IAS and to identify priority IAS, pathways, or sites for action and management.

While knowledge and resources to address the challenges of IAS have increased exponentially over the last several decades, the available knowledge and technologies to manage biological invasions are not adequately reflected in global, regional, and national policies and strategies. Large gaps between science, management, and policy at various geopolitical scales still exist and necessitate an urgent need for more integrative approach across multiple scales and multiple stakeholder groups to bridge those gaps and reduce the impacts of biological invasions on biodiversity and human well-being. The modular global strategy model proposed in this chapter can be visualized as a set of Russian dolls – dolls of different sizes that nest inside one another. The different dolls represent different legal instruments and voluntary measures that together define the overall strategy for a particular region or the globe. Some countries may adopt many or all aspects of the strategy and will have many “dolls within dolls,” while other nations will have fewer. Yet all the different “dolls” or strategies adopted by nations work together toward the same goal of reducing biological invasions and minimizing their impacts. Importantly, the “dolls” or strategies must be maintained to ensure that they continue to fit into other larger and smaller “dolls” or strategies and that others fit into them. In many cases, component laws and policies are modified without adequate attention being given to “parent” and “offspring” instruments, resulting in conflicting regulations and/or important issues “falling between the cracks” and being left out of policies.

This proposed approach for IAS is thus inclusive, adaptive, and flexible and moves toward global strategies for better preventing and managing biological invasions. Clearly, the world has a long way to go in terms of achieving such comprehensive global strategies. Nonetheless, as

existing networks that focus on biological invasions mature (Table 16.1) and new networks come online, and as partnerships between such networks with existing intergovernmental and international organizations with an IAS focus (Table 16.2) strengthen, achieving effective global strategies will become an attainable reality.

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A Future Planet of Weeds?

17

Daniel Simberloff

Abstract

In some habitats (e.g., grasslands and wetlands), a predicted homogeneous mass of dominant non-native plants is in the process of being realized. Although certain species have achieved widespread non-native distributions, the same ones are not always among the most common invaders in all regions to which they have been introduced. For forests, an “inertia” largely owing to the longevity of dominant native trees has retarded homogenization and may do so for another century or more, as disturbances and seed dispersal provide ever more opportunities for non-natives to replace natives. However, without a substantial new relationship between humankind and natural habitats and their native biodiversity, as well as the continued development of promising new management tools, it is difficult to be optimistic that, within a millennium, forests will not be dominated in many regions by non-native species. Available regional data are on numbers of non-native species in particular sites. Such information is suggestive, but to evaluate the prediction that the Earth will become a “planet of weeds” and to determine at what rate such a transition is occurring

would require many more data on areal coverage by particular species. Such data are currently gathered almost exclusively over very small areas as parts of local ecological studies.

Keywords

Climate change · Disturbance · eDNA · Fire regime · Forest · Gene drive · Gene silencing · Inertia · Plant invasion · Transgene

17.1 Introduction

Two decades ago, nature writer David Quammen (1998) coined the phrase “planet of weeds” to predict the long-term result of biological invasions. He foresaw that 150 years in the future large parts of the Earth would still be green, and many locations would still house large numbers of species, but they would be the same species – the globally invading “weeds.” By “weeds,” Quammen (1998) meant weedy animals as well as plants, but he pointed particularly to the destruction of forests and cited many prominent invasive plants – tamarisk (*Tamarix* spp.), Australian paperbark (*Melaleuca quinque-neria*), water hyacinth (*Eichhornia crassipes*), kudzu (*Pueraria montana*), cheatgrass (*Bromus tectorum*), European buckthorn (*Rhamnus cathartica*), spotted knapweed (*Centaurea*

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stoebe), Russian thistle (*Salsola* spp.), leafy spurge (*Euphorbia esula*), purple loosestrife (*Lythrum salicaria*), and cordgrass (*Spartina* spp.). At the same time, and independently, plant ecologist Francis Putz (1997, 1998, 2000) popularized the term “Homogeocene,” first proposed by (Guerrant 1992), to capture what he predicted to be an ecologically diminished future in Florida and beyond, emphasizing the spread of invasive non-native plants – cogongrass (*Imperata cylindrica*), water hyacinth, hydrilla (*Hydrilla verticillata*), and Australian paperbark in Florida and eucalypts (*Eucalyptus* spp.), pines (*Pinus* spp.), European poplars (*Populus* spp.), and Asian willows (*Salix* spp.) in South Africa. This notion of homogenization has become a component of the growing concern with massive species extinction, especially the role of invasions in global biodiversity loss, with dominating invaders the “winners” and declining or extinguished native species the “losers” (McKinney and Lockwood 1999; Lockwood and McKinney 2001).

17.2 Insufficient Data

Both metaphors conjure up an image of an endless landscape dominated by non-native plants, with certain of these species common over large swaths of the Earth. However, despite a large and growing literature predicting the trajectory of plant invasions, the predictions do not directly address this planet-of-weeds image and instead largely focus on the future spread of particular species or the number of non-native species that will be found in particular large regions. For instance, the exhaustive analysis by Chytrý et al. (2012) predicting trends in plant invasions in Europe in 2020, 2050, and 2080 in light of different future land-use scenarios characterizes level of invasion in terms of percentages of non-native species among all plant species in 10 × 10 minute cells of Europe (<1, 1–3, 3–5, >5%). Most scenarios predicted an increase in invasion level thus defined for most of Europe. One can reasonably hypothesize that a greater percentage of the flora consisting of non-native species will correlate with greater areal coverage, but this would

still simply be a hypothesis. Likewise, the temporal trend of rapid increase in invasive plants in Europe depicted from ca. 1600 to 2000 by Lambdon et al. (2008) is in terms of numbers of species recorded as alien to at least one European nation.

Similarly, Bradley et al. (2015) divided the continental United States into cells of 50 × 50 km and characterized degree of invasion by the number of species of non-native plants (divided into categories of “alien” and “invasive”) in each cell. Their aim was to determine whether native or non-native plants have greater potential distributions, as predicted by a custom species distribution model based on the climate of the occupied cells. The main finding was that, on average, non-native species have greater potential ranges than do native species, in terms of occupied cells. Again, it could be reasonably hypothesized that greater areal range would correlate with greater areal coverage by non-natives in the future, but this would be only a hypothesis. The type of data needed to characterize degree of invasion and to predict future degree of invasion in the planet-of-weeds sense would be mean cover, species by species, however estimated (Damgaard 2014). Such data are commonly collected by ecologists at small scales, often laboriously, but they are not gathered regionally. Perhaps with the continuing development of remote sensing technology (see below), data of this sort will be accessible over vast areas.

For most continents, data even to approximate current species richness by map cell, much less areal coverage, are unavailable (e.g., Zenni et al. [this volume](#), Chap. 9). Richardson et al. (2020) provide possibly the closest approximation to a baseline for assessing the planet-of-weeds prediction, citing research conducted in 1996–1997 by Le Maitre et al. (2000) concluding that ca. 8% (ca. 10 million ha) of South Africa was occupied to some extent by ca. 180 mapped non-native plant species, with ca. 1.4% (1.76 million ha) significantly impacted. In 2018, the Southern African Plant Invaders Atlas showed 82% of South Africa’s quarter-degree grid cells occupied by species from among 739 non-native plant species recorded, perhaps suggesting an increase

from 1996–1997. However, Richardson et al. (2020) emphasize that the survey was not designed to provide an in-depth estimate of the extent of invasions, and the analysis focuses on numbers of native and non-native species in various cells. Richardson et al. (this volume, Chap. 11) observe that many invasive species that are widespread and abundant in South Africa are emerging weeds across much of the rest of Africa, which is currently generally much less invaded, and that many of these species, including trees invasive in South Africa, will likely spread widely in the continent, facilitated by agroforestry and various kinds of disturbance.

17.3 Increasing Numbers and Spread of Invasions

Certainly, the number of invasions has accelerated over the past several decades (Seebens et al. 2017, 2018) and is likely to continue to do so for the foreseeable future, for several main reasons. Most important for plant invasions is habitat destruction and transformation (Jenkins and Pimm 2003). Many native species are maladapted to the resultant changed habitats, but these are suitable habitats for other species, including many invaders from elsewhere. The habitat change is the driver for these introduced plants, which are the passengers (MacDougall and Turkington 2005); some of these plant invaders then become backseat drivers, inducing further losses of native plant species by various means, such as changing fire or nutrient regimes (Bauer 2012). Further, the disturbance of the transformation itself and the disturbance regime of many of the resulting habitats (e.g., agriculture, commercial forestry) favor many of the invading species over natives (Elton 1958; Davis et al. 2000; Hierro et al. 2006; Lembrechts et al. 2016); indeed, thriving in a disturbed habitat is one defining characteristic of the colloquial term “weedy.”

The key role of increased trade and travel in both deliberate and inadvertent invasions generally and plant invasions in particular cannot be doubted (Seebens et al. 2015; van Kleunen et al.

2018). For instance, transport of commodities accounted for 81% of non-native weeds intercepted at US ports of entry in the 1980s (US Congress OTA 1993). Container cargo shipped by sea is predicted to rise from 182 million TEU (20-foot equivalent unit; the standard container) in 2016 to between 464 million and 858 million TEU in 2066 (Saxon and Stone 2017), while air cargo (freight plus mail) is predicted to expand from 256 billion RTK (revenue ton-kilometers) in 2017 to 584 billion RTK IN 2037 (Crabtree et al. 2018). These estimates preceded the COVID-19 pandemic, and similar statistics were depressed to varying extents for up to a decade following the “Great Recession” of 2007–2009, but they give a sense that this driver of plant invasions will increase substantially, at least in the next few decades.

Climate change will also exacerbate the spread of non-native plant species. The first use of a species distribution model to predict the spread of an introduced species, an Australian eucalyptus in Africa, was by Booth (1985), but papers by Bradley et al. (2009, 2010) using MaxEnt and the Mahalanobis distance method and various climate projection models to predict the range of several non-native weeds in the United States precipitated a wave of similar efforts for other introduced species that shows no signs of abating. Most such modeling efforts predict spread. For instance, Bradley et al. (2009, 2010) predicted substantial spread by 2100 of yellow starthistle (*Centaurea solstitialis*), tamarisk, kudzu, privet (*Ligustrum sinense* and *L. vulgare*), and cogongrass, range shift of cheatgrass and spotted knapweed, and contraction of the range of leafy spurge. Much further research has explored species distribution models combining climate change effects on species ranges with impacts of other factors, such as the presence or absence of other species (e.g., Wisz et al. 2013; Anderson 2017). Taking a different tack, Leishman and Gallagher (2015) surveyed the basic biology of many native and non-native plants and similarly concluded that predicted climate change will likely increase invasion by reducing resilience of native vegetation. Others have studied particular invasive plants and found

that predicted temperature change will enhance their performance and likely increase their invasiveness (e.g., Tietze et al. 2019). Ziska ([this volume](#), Chap. 4) describes how predicted rise in CO₂ both independently and in concert with temperature change will likely lead to the expansion of at least some non-native plant species. Though it is apparent that the response of non-native plants to climate change will be species- and context-specific, it appears clear that the net effect will be more range and abundance increases than decreases. In addition, global climate change will cause many native species' ranges to shift and often to expand (Inderjit et al. 2017), which will further enhance homogenization.

The sum of evidence on these three key factors – habitat destruction and transformation, trade and travel, and climate change – strongly suggests an overall increase in the number and range of plant invaders over the next century (cf. Young et al. [this volume](#), Chap. 2).

17.4 A Future Planet of Weeds?

Although the number of non-native plant species will surely increase in most if not all locations over the next century for the reasons just stated and perhaps others, the planet-of-weeds image of an endless, homogeneous forest landscape dominated by relatively few invasive species is unlikely to come to pass in this century and perhaps much longer, even in the absence of potential measures and technologies to hinder and even push back the spread. Pearsall (1959) was perhaps the first to relate the notion of biological inertia to vegetation change in the face of invasions in a review of Elton's classic early invasion book (Elton 1958), opining that dense native vegetation would largely restrict invasion to sites where disturbance removed the natives. He also suggested that at least 500 years would be required for "appreciable" change in climax forest species composition in the absence of anthropogenic disturbance. Von Holle et al. (2003) proposed a sort of vegetational inertia, observing that, because of the longevity of many forest trees and the legacy of their presence (e.g., soil proper-

ties), even an aggressive invader might need centuries to replace a less well-adapted native species, supporting the contention of Gilbert and Levine (2013), based on metapopulation modeling and observation of an invaded California grassland, of an extinction debt generated by invasive plants that may take centuries to be paid. Soil seed banks for some species can persist for up to 400 years (Downey and Richardson 2016). Many Holocene palynological studies depict a centuries- or even millennia-long slog for climate-induced range expansion of native tree species, perhaps requiring disturbances like tree falls or fires to remove retreating native species and partly determined by the dispersal characteristics of the expanding species (Davis 1986; Davis et al. 1986; Von Holle et al. 2003). Such range expansions by native species have sometimes been called "invasions" (e.g., Davis 1987). Such "native invasions" in the short term have usually been triggered by anthropogenic changes (Simberloff 2011), although range changes of both non-native and native species are affected by current anthropogenic climate change and may share certain characteristics (Inderjit et al. 2017).

It is noteworthy that Early et al. (2016) find just one-sixth of the global land surface highly vulnerable to invasion by non-natives based on their assessment of the predicted twenty-first-century globalization and environmental change patterns and national capacities to prevent and manage invasions. Theirs is a very broad-brush, big-picture forecast, but their map (their Fig. 1) depicts large areas that include many biodiversity hotspots as having low or very low invasion threat (which does not minimize the fact that several hotspots are also in regions assessed as having high threat of invasion). Although the data and predictions of Early et al. (2016) do not directly address the planet-of-weeds image, they at least suggest that large sections of the globe will not accord with that image in this century.

Surely many of us have had the experience of hiking in large forested natural areas and seeing myriad invasive non-native plants, sometimes even dominant ones, near trails or otherwise disturbed areas—then hiking into roadless, more

remote areas—and seeing few if any non-natives. For instance, the Great Smoky Mountains National Park in the southeastern United States contains ca. 380 non-native plants species, very largely in old homesites or disturbed areas such as road verges, burns, or construction sites (Jenkins and Johnson 2009) and often very evident near heavily trafficked areas. However, one can hike into roadless areas with minimally used trails, quickly be surrounded by native vegetation, and struggle to find a single non-native plant. Several non-native plant species do invade closed forest in the Great Smoky Mountains National Park, notably *Celastrus orbiculatus* and *Microstegium vimineum* (Jenkins and Johnson 2009), and elsewhere may invade even undisturbed forest (Martin et al. 2009; Dechoum et al. 2015). Nevertheless, most intact forest is relatively uninvaded. How long the “inertia” described by Pearsall (1959) will impede invasion in the face of normal disturbances such as tree falls and the forces cited above that will be bringing ever more non-native species is unknown, but I doubt that we will see a planet of weeds in this century. However, I suspect that, without novel and effective management approaches (discussed below) and the willingness to implement a global strategy with effective national policies (Meyerson et al. [this volume](#), Chap 16), five or ten centuries from now, Quammen’s (1998) metaphor will have been realized for forests.

With respect to invasion, forests, which comprise ca. 31% of the Earth’s land surface (FAO and UNEP 2020), may be the most inertial of the major vegetation types, largely because of the longevity and bulk biomass of the dominant species. Grasslands cover about 40% of the land surface (Suttie et al. 2005). As with forests, although several studies tally the number of non-native species in particular sites, areal coverage is much less frequently recorded except over small areas. However, in several regions, non-native plants have come to dominate large areas (Clark 1956; Seastedt and Pyšek 2011); North American grasslands are a prime example (cf. Mack 1989). Even Darwin (1839) marveled at huge expanses of Patagonian grasslands utterly dominated by two

introduced plants. Key drivers of the increasing dominance of grasslands by non-native plants are other global changes such as nutrient enrichment and climate (Flores-Moreno et al. 2016) and land-use changes, especially grazers (Mack 1989), as well as changed fire regimes (D’Antonio and Vitousek 1992). Complex and regionally and temporally varying interactions among all of these factors have already led large grasslands to contribute to a planet of weeds, with a relatively small number of non-native species dominant, although different ones prevail in different regions (Seastedt and Pyšek 2011). Wetlands cover about 6% of the Earth’s land surface (Reis et al. 2017). As with forests and grasslands, several records exist of number of non-native plant species in particular sites, but tallies of areal extent dominated by invaders are restricted to small areas. Nevertheless, many accounts describe vast wetland areas dominated by non-native *Spartina* spp. (Strong and Ayres 2013), *Phragmites australis* (Lambert et al. 2010; Saltonstall and Meyerson 2016), *Phalaris arundinacea* (Spyreas et al. 2010), *Arundo donax* (Lambert et al. 2010), and other plants. As in forests and grasslands, the invasion of non-native plants into wetlands interacts with other global changes; for wetlands, land-use change and nutrient increase are major drivers of invasion (Chen 2019).

It is possible, of course, that totally new forces or dramatic changes in existing processes may increase the rate at which non-native plants dominate forests, grasslands, wetlands, and other habitats. For grasslands, fires partly spurred by invasive non-native plants themselves have already proven to be a major factor (D’Antonio and Vitousek 1992). Increasing fire severity owing to climate change plus previous fire exclusion has already led to “mega-fires” of greatly increased area and intensity in forests worldwide (Stephens et al. 2014), with the role of climate change in mega-fires of the western United States firmly established (Abatzoglou and Williams 2016; Parks and Abatzoglou 2020) and suggestions of similar future changes in fire regimes of the southeastern United States (Stephens et al. 2014). Such events can lead to loss of forest habi-

tat entirely, invasion of non-native plants better adapted to the new fire regime, or both, but the recency of scientific study of the phenomenon does not yet permit a firm prediction of its contribution to a planet of weeds. One might also speculate on the possibility that a pathogen or insect pest introduced in the future might devastate a dominant native forest tree species and precipitate an invasive takeover by a non-native species currently present but relatively innocuous. In the distant past, such a devastating pathogen or insect invasion would have led to replacement by existing native species because non-native competitors were not waiting in the wings. The great decline of hemlock (*Tsuga* spp.) in eastern North America about 5000 years ago is a prime example (Davis 1981a, b; Fuller 1998). Even with non-native trees present, the rapid virtual elimination by chestnut blight (*Cryphonectria parasitica*) of American chestnut (*Castanea dentata*) from forests of the eastern United States during the first half of the twentieth century led to its replacement by native species, especially oaks (*Quercus*; McCormick and Platt 1980). No evidence suggests that the current ongoing elimination in eastern North America of native ash (*Fraxinus* spp.) by the introduced emerald ash borer (*Agilus planipennis*; Herms and McCullough 2014) and hemlock (*Tsuga* spp.) by the introduced hemlock woolly adelgid (*Adelges tsugae*; Orwig et al. 2008) is leading to widespread replacement by non-native species, although in the long term, such a replacement for these or other tree species attacked by introduced pathogens or insects cannot be excluded.

17.5 Existing and New Technologies that Could Help Prevent a Planet of Weeds

As observed by Downey and Richardson (2016), aggressive management can forestall extinction and, if effective, could surely at least delay realization of the planet of weeds. Incremental improvements in existing technologies or completely new approaches (Simberloff et al. 2018)

could transform what seems to most of us now like a losing battle into at least a persistent stalemate. In particular, a number of proposed technologies involving molecular genetics could be game changers.

Early detection and rapid response are the first step in preventing non-native arrivals from becoming invasive (Meyerson and Simberloff 2020). Several new technologies can greatly improve early detection of non-native plants and are already in use to some extent. Citizen scientists (or non-scientists!) armed with smartphones and appropriate apps, such as iNaturalist and IveGot1, can multiply the detection capability enormously (Martinez et al. 2020; Dehnen-Schmutz and Novoa [this volume](#), Chap 15). The key is for such apps to be associated with a stable program to register and evaluate the images, such as EDDMaps (Barger et al. 2011). Unmanned aerial vehicles (UAVs, drones) can carry cameras and other sensors and search large areas and difficult terrain; they have detected, i.a., yellow flag iris (*Iris pseudacorus*), silk oak trees (*Grevillea robusta*), and invasive grasses (Martinez et al. 2020). LiDAR has already been used to detect invasive plants (e.g., Barbosa et al. 2016), and drones can also carry new lightweight LiDAR sensors (Martinez et al. 2020). Nanosatellite constellations may also be able to replace drones as well as larger satellites for invasive plant detection purposes (Martinez et al. 2020).

Detection of invasive aquatic animals, especially in freshwater, has rapidly been revolutionized by the advent of environmental DNA, although plants and terrestrial species generally have presented particular challenges (Cristescu and Hebert 2018). However, several research teams have recently reported using eDNA to detect invasive aquatic plants (Dehnen-Schmutz and Novoa [this volume](#), Chap 15), and the recent detection of terrestrial plants from honey bee pollen pellets (Tremblay et al. 2019) suggests that the ambit of eDNA methods for early detection of non-native plants will broaden.

Once an invasive plant population is established, many long-established technologies may be used to control or even eradicate it, primarily the traditional methods of mechanical or physical

control, herbicides, and biological control. Each of these three approaches can boast of successes, but all have also failed. However, incremental technological advances accrue in all three areas (Simberloff 2014; Simberloff et al. 2018), and occasionally a larger advance renders formerly intractable invasions tractable. Ballistic herbicide technology employing helicopters is an example and has been used successfully in mountainous terrain in the Hawaiian Islands and Santa Cruz Island, California (Leary et al. 2012; Cory and Knapp 2014). Organized teams of volunteer citizens have also contributed substantially to management of established invasive plants, especially engaging in mechanical or physical control (e.g., Dechoum et al. 2018). Without ongoing monitoring and management, if an invasive population is not completely eradicated, reinvasion can occur, and eradicated or greatly reduced invasive plants may be replaced by other non-natives (the “treadmill effect”; Thomas and Reid 2007).

Substantial interest in using double-stranded RNA (dsRNA)-mediated gene silencing (RNAi) to control animal invaders has built on an explosion of research on its possible use in medicine (Titze-de-Almeida et al. 2017). Much of the animal research targets agricultural pests, and some methods combine gene silencing and manipulating the genome. Most effort has gone into producing transgenic crop plants that produce dsRNAs specific to a particular insect (Zotti et al. 2018). For instance, Monsanto has modified the genome of maize (*Zea mays*) such that it silences genes in western corn rootworm (*Diabrotica virgifera virgifera*) when the insect attacks the plant (Bachman et al. 2013; Zhang et al. 2017; Zhu 2017), and DuPont applied for a patent for a similar approach using gene silencing to control pest stinkbugs, such as the invasive brown marmorated stinkbug, *Halyomorpha halys* (McGonigle et al. 2016). An alternative gene silencing method not entailing the use of transgenes is to spray or otherwise topically apply to plant leaves dsRNA specific to the target insect or pathogen. This variant has proven more challenging because of the relative instability of dsRNA sprayed on plants, but there is progress in solving this problem by loading the dsRNA on designer clay

nanosheets, whereby the dsRNA does not wash off and remains stable for at least a month (Zotti et al. 2018). It has also been demonstrated that topically applied dsRNA is translocated to untreated parts of the plant (Zotti et al. 2018). These are not the only ways in which gene silencing is being developed to control animals. Leonard et al. (2020) have modified the genome of a bacterium (*Snodgrassella alvi*) that is a gut symbiont of the honey bee (*Apis mellifera*) to express dsRNA sequences for genes of the parasitic varroa mite (*Varroa destructor*), thus killing the mite by activating its RNAi mechanism to destroy those sequences. Savaya-Alkalay et al. (2018) have proposed using gene silencing to produce all-male prawns as a biological control for invasive snails.

In contrast to these developing methods to use gene silencing on invasive animals, I am aware of only one such effort on plants, a US government-funded project to control invasive *Phragmites australis* in which genes critical for such important features such as flowering, seed set, and photosynthesis are targeted (Martinez et al. 2020). The use of a transgene to effect gene silencing in a plant would not be an option, as natural selection would quickly eliminate it, but repeated topical application would be feasible, as has been demonstrated for control of phytophagous insects and plant pathogens as described above.

The notion of using transgenes to control invasive animals was widely bruited beginning in the early 2000s (Gould 2008) and burst into public view with Oxitec’s Friendly™ *Aedes aegypti* mosquito, which carries a transgene inactivated by tetracycline but renders females flightless (i.e., lethal in nature) when reared on a diet without tetracycline (Fu et al. 2010). Reports of field tests of the mosquito on Grand Cayman Island raised concern about lack of regulation (Angulo and Gilna 2008) and unintended consequences (Enserink 2010), but as Zika virus spread to the western hemisphere, Oxitec mosquitoes were released in great number and caused great declines in local numbers of *Aedes aegypti* (Servick 2019), with little controversy (Rutkin 2016; Servick 2016). The recent discovery in a wild *Aedes aegypti* population in Brazil that a

small percentage of individuals carry genes (but not the transgene) of the Oxitec mosquito, proving that at least some offspring of the Oxitec mosquito survive (Evans et al. 2019), has generated new controversy over the safety of the approach (Servick 2019). Nevertheless, Oxitec is developing similar versions in seven other insects, including major invaders *Ceratitis capitata*, *Drosophila suzukii*, *Spodoptera frugiperda*, *Plutella xylostella*, and *Anopheles stephensi* (<https://www.oxitec.com/en/our-technology>, accessed Jan. 30, 2020). Although most of the transgene action on invasive animals is aimed at insects, projects targeting other invasive animals are in various stages of development (Harvey-Samuel et al. 2017): Channel catfish (*Ictalurus punctatus*), common carp (*Cyprinus carpio*), and Pacific oyster (*Crassostrea gigas*).

The use of transgenes in plants was first reported in 1983 [a bacterial antibiotic resistance gene in tobacco (*Nicotiana tabacum*); de Framond et al. 1983], and many transgenic versions of plant species exist (Rani and Usha 2013; Low et al. 2018). Transgenic plants have been created for pest resistance, herbicide resistance, drought tolerance, salt tolerance, increased yield, and greater nutritional value and as bioreactors for various proteins. Transgenes do **not** appear to have been employed as in animals to attempt to control an invasive plant species. Remarkably, transgenic versions of several plants prominent in the invasion literature have been produced, but not for the purpose of controlling an invasion. For instance, Kim et al. (2013) produced transgenic *Phragmites australis* (reported as *P. communis*) as part of a project to reduce lignin content to facilitate the use of the species as a biofuel feedstock, and Czakó et al. (2006) used a transgene to improve the mercury phytoremediation performance of *Spartina alterniflora*, parent of the invasive hybrids *S. anglica* and *S. foliosa* x *alterniflora* (Strong and Ayres 2013). The entire approach of spread of a transgene requires sexual reproduction, and the fact that many plants can reproduce vegetatively of course complicates an attempt to develop such a strategy but perhaps does not close it off completely. Ingenuity and effort may well fashion methods incorporating

transgenes, possibly in hybrid methods, such as the combination of gene silencing with transgenes described above. Gould (2008) suggested several ways in which transgenes might effectively control Scotch broom (*Cytisus scoparius*), but to my knowledge, none have been pursued.

As CRISPR-Cas9 gene editing technology became widely researched and fine-tuned for use in medicine and agriculture (e.g., Hu et al. 2018; Cohen 2018), Esvelt et al. (2014) pointed to its possible use in control of invasive species. Harvey-Samuel et al. (2017) and Moro et al. (2018) review a variety of ways in which RNA-guided gene drives, particularly CRISPR-Cas9, can be used, generally in conjunction with transgenes, to control or eradicate invasive animal populations. Some projects are well resourced and have generated substantial research, such as Target Malaria for *Anopheles* mosquitoes (<https://targetmalaria.org/>) and GBIRD for invasive rodents (<https://www.geneticbiocontrol.org/>). A striking recent project supported by the US Bureau of Reclamation aims to introduce a transmissible cancer found in soft-shell clams (*Mya arenaria*) into zebra mussels, potentially with the aid of CRISPR-Cas9, to silence a tumor-suppressing gene (<https://www.usbr.gov/newsroom/newsrelease/detail.cfm?RecordID=63426>, <https://invasivemusselcollaborative.net/wp-content/uploads/2019/03/Suhr-Biomilab-Eradication-of-Invasive-Mussels.pdf>).

The advent of CRISPR technology fostered a remarkably rapid development of the system for use in plants, with production of many CRISPR-edited species (Ma et al. 2016; Puchta 2017). However, virtually all of them are aimed at either increasing agricultural production or purely scientific advancement (the latter particularly with *Arabidopsis thaliana*). Despite suggestions that various genetic methods would in principle at least limit and might possibly eradicate invasive plant populations (e.g., Gould 2008; Hodgins et al. 2009) and that these would appear to be rendered more feasible by CRISPR technology, such research has not been a focus of CRISPR researchers, and certainly not to the extent that it has captured the attention of scientists addressing animal invasions (Barrett et al. 2019). Both facul-

tative vegetative reproduction and selfing would act to limit the spread of a driven gene (Drury et al. 2017), and the presence of a soil seed bank would slow the spread of a driven gene by continually introducing wild-type alleles (Barrett et al. 2019). And, as with animals, natural selection will always be engendered to counteract actions of a driven detrimental gene in a race between extinction and the evolution of resistance to the drive (Noble et al. 2018). Nevertheless, for many plant species, such effects would not necessarily prevent a successful project (Barrett et al. 2019), and Neve (2018) has outlined the prospects and challenges for employing gene drives to manage and possibly locally eradicate agricultural weeds. Gene drives have spawned controversy because of the possibility they will extinguish targeted populations or even non-target species (Anon. 2016; National Academies 2016; Callaway 2018), but the increasing accessibility of gene drive technology ensures that they will be used in nature, possibly for nefarious purposes (Cohen 2016; Baumgaertner 2018), and that such use includes being employed against invasive non-native species.

17.6 Conclusion

Will the Earth ultimately be a homogenized planet of weeds, and, if so, when? Surely more and more of the surface of the planet will contain more and more non-native plant species, and some further fraction will be dominated by them, so areal coverage by non-natives will increase. The Earth will still be green, as Quammen (1998) predicted. How much of the area will be dominated by global non-native weeds? Certainly, the global strategy advanced by Meyerson et al. (this volume, Chap. 16) would slow the weedy juggernaut, and the various management tools already in place or on the horizon could further retard its advance and might even reverse it in places. Will such a global strategy be implemented? It is difficult to be optimistic, especially in an era of growing nationalism; the response to global climate change also does not inspire confidence. Some fraction of the various genetic approaches

currently being actively researched, and other technologies we have not yet dreamed of, will be employed to some effect. In 150 years (Quammen's prediction), I suspect a majority of the forested Earth will still be dominated by native plants, but the forces arrayed against conservation of native ecosystems seem so massive and inexorable that it is hard to be optimistic that these will persist for a millennium. The process in grasslands is already well underway.

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