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Montserrat Vilà
Philip E. Hulme *Editors*

Impact of Biological Invasions on Ecosystem Services

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Biological Invasions represent one of those rare themes that cut across the disciplines of academic biology, while having profound environmental, philosophical, socioeconomic, and legislative implications at a global scale. There can be no doubt that biological invasions represent the single greatest threat to biodiversity past the activities of humankind itself. The implications are far reaching. Novel ecological and evolutionary forces are now directing the future expression of life itself, as native species and the communities that they comprise contend with invading species. The rules of the game have been suddenly and irrevocably changed.

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Editors

Impact of Biological Invasions on Ecosystem Services

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EUROPEAN COOPERATION
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ALIEN
Challenge

Springer

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To our families who give us the time to learn

Foreword by Braulio Ferreira de Souza Dias

Invasive alien species are considered a direct driver of biodiversity loss, a key issue affecting all major biomes. Invasive alien species are also known to cost our economies billions of dollars each year. The cost arises from economic loss in the agriculture, forestry, energy, and health sectors, negative effects on the delivery of ecosystem services, and the price tag for control and eradication efforts once invasive alien species are established.

Article 8h of the Convention of Biological Diversity (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*" to address the issue of invasive alien species. In 2002 the CBD Parties adopted the guidelines for the prevention, eradication, and control of invasive alien species, and at the tenth meeting of the Conference of the Parties (COP) to the CBD, held in Nagoya, Aichi Prefecture, Japan in 2010, the Parties adopted the Strategic Plan for Biodiversity 2011-2020 and its 20 Aichi Biodiversity Targets, including 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*." Furthermore, in 2015 the United Nations General Assembly adopted the 2030 Sustainable Development Agenda, and agreed for target 15.8 on invasive alien species to be achieved by 2020, the same year as targeted for the Aichi Biodiversity Target 9. These global objectives reinforce the urgency of appropriate invasive alien species management as a contribution to sustainable development.

To achieve these targets, the CBD, through its Subsidiary Body of Scientific, Technical and Technological Advice (SBSTTA) and the COP, has continued to develop international guidance and possible response measures. As a result, many countries have advanced in developing strategies and putting measures in place to prevent invasions and minimize the negative impacts of invasive alien species. Nonetheless, the fourth edition of *Global Biodiversity Outlook* (GBO-4) warns that even though there has been significant progress toward meeting some Aichi targets, the overall rate of invasions has shown no sign of slowing down.

The increase in international trade, travel, and related modern technology intensifies the risk of entry and spread of alien species that become invasive in many different biogeographic regions across the world. If we do not take prompt action, the known and potential impacts of invasive alien species on biodiversity and ecosystem services can cast a shadow on the sustainable development agenda. A key approach is the analysis of scientific evidence of high-impact invasive species and the analysis of introduction pathways as a means to prioritize these and to apply effective preventive or control measures.

To that end, information on the impacts caused by invasive alien species on biodiversity, ecosystem services, and functions is essential for assessing risks from biological invasion to both economy and environment. The publication of *Impact of Biological Invasions on Ecosystem Services* comes at a critical time when countries seek to accelerate actions to achieve the Aichi Biodiversity Targets. It enhances awareness about the impacts of invasive alien species on biodiversity and related issues such as food and water security, climate adaptation and mitigation, or the sustainable supply of biological materials, among others. With continuous monitoring and sharing of information regarding the global impacts of invasive alien species on biodiversity and ecosystem services, countries will be in a better position to prevent biological invasions and thereby achieve related sustainable development ambitions.

I would like to encourage experts, land, water, and resource managers, and control officers to widely use the knowledge compiled in this publication for the sustainable management of ecosystems, and thus ensure that our biodiversity can continue to generate its invaluable and irreplaceable benefits for future generations.

Convention on Biological Diversity
Montreal, QC, Canada

Braulio Ferreira de Souza Dias

Foreword by Piero Genovesi

The current dramatic extinction crisis and the increasing pace of loss of biodiversity require urgent action by the global community, whose efforts have so far proven to be inadequate. Addressing the global threats to biodiversity is essential not only for preserving wild species and ecosystems but also for protecting our livelihood, which largely depends on healthy natural systems.

Biological invasions are indeed one of the major drivers of change at the global scale, and one for which action has been so far particularly sparse. To guide policy, it is therefore essential to better understand the effects of the increasing introduction of invasive species: important not only in terms of biodiversity loss but also with regard to effects these invasions have on our lives. Indeed, this is a primary concern for decision makers, particularly in developing areas of the world.

This book, authored by an impressive group of leading experts on the impacts of non-native species, presents the first comprehensive overview of how non-native species alter the services to humans provided by natural ecosystems and includes an in-depth analysis of the patterns and trends of these impacts. The volume provides a much-needed up-to-date picture of the severe effects of non-native species on the quality and quantity of products obtained from ecosystems, such as crops, timber, and fish stocks. It also explores the effects of biological invasions on the regulation of ecosystems, as in the case of disruptive effects of non-native species on water regulation, describing the impact on erosion, water quality, and other key services associated with freshwater. The book also discusses the impacts of biological invasions on health, analysing the effects of the expansion of non-native mosquitoes and of the consequent spread of many diseases, for example. Last but not least, this book addresses the impacts of invasions on the cultural services provided by ecosystems, analysing the effects on recreational and aesthetic values.

This volume, structured in four sections, not only analyses the known impacts of nonnative species on all ecosystem services but also includes a synthesis of the main results that is particularly valuable for defining the information gaps on this aspect and, eventually, for informing decision makers.

The merit of this excellent text is to present the first-ever analysis of the impacts of biological invasions on ecosystem services, with scientific rigour, but also in a form that can be understood by different audiences, from scientists to students to practitioners and decision makers. This information is the key to informing the entire society on the need and importance of addressing biological invasions, showing that protecting nature from this threat also preserves our life.

Piero Genovesi

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Rome, Italy

Foreword by Helen E. Roy

Biological invasions are widely considered as a major threat to biodiversity and ecosystem function. However, there is a need to improve the understanding of impacts of biological invasions and to provide robust empirical evidence to underpin decision making. There is an increasing need to consider the impacts of an alien species at various scales, recognizing the complexity of interactions within communities and ecosystems. Indeed, the importance of impacts of alien species on ecosystem function and consequently ecosystem services has been highlighted within the new EU Regulation on Invasive Alien Species. A number of studies have demonstrated the challenges of quantifying impacts on ecosystem services, not least the need for a consolidated framework in which to define the types of ecosystem services. Therefore, this book represents a timely contribution, providing a synthesis of research to advance understanding of impacts of alien species.

It is exciting to see the range of topics covered within this book and spanning the defined ecosystem services: supporting, provisioning, regulating, and cultural. From changes in primary production to carbon sequestration to the use of alien species in poverty alleviation, this book provides a synthesis that will be of value to invasion biologists but also of considerable interest to many others. As an example, concerns about the decline of pollinating insects are echoed around the world. It is important to reflect on the role of invasive alien species alongside other drivers of change in contributing to the observed declines. Similarly, research has been emerging on the way in which the addition of an alien species to a community has profound aboveground and belowground effects on biogeochemical cycles. The chapters in this book reviewing such innovative research will be of critical importance in advancing our understanding.

Alien species, by definition, are species on the move—often crossing continents. The need for collaborations across countries and between academics, practitioners, and policy makers is critical. This book, with 50 contributors spanning 18 countries, highlights the inspiring collaborative nature of research on biological invasions. It is a pleasure to be able to provide support to this network of international biologists through the EU-funded COST Action ALIEN Challenge (www.brc.ac.uk/alien-challenge/home).

NERC Centre for Ecology & Hydrology Helen E. Roy
Wallingford, UK

Preface

The field of biological invasions arouses considerable interest within different sectors of society. Many scientists are curious to understand how introduced species have been moved across continents by humans, why these species become established in a new region, and what the consequences might be of their interaction with native species and recipient ecosystems. Ecologists and conservationists have for many decades been concerned about the ecological impacts of non-native species on biodiversity as well as on the loss of quality of invaded ecosystems. For example, in Europe there are more than 1000 non-native species with documented ecological impacts.

The terminology regarding biological invasions has been the focus of much discussion. In this book, we have mostly used the term 'non-native' (synonyms include alien, non-indigenous, exotic) throughout to describe species introduced to new regions by human activities. Furthermore, we have restricted the use of the term 'invasive species' to the subset of non-natives that have impacts on ecosystem services.

Harmful non-native species are not only present in natural ecosystems but are also found in systems that are the key to sustaining our livelihood, including agricultural lands and urban areas. Farmers, veterinarians, epidemiologists, medical professionals, and civil engineers are involved in avoiding, detecting, and managing weeds, pests, and pathogens that interfere with crops, livestock production, infrastructure, and public health. All these impacts have direct economic costs. Such cross-sectorial impacts require a multidisciplinary approach to the field of biological invasions to evaluate and mitigate the consequences of harmful non-native species.

Despite these concerns, both the numbers and distributions of non-native species continue to increase in most countries of the world to the extent that the biogeographic distinctiveness of different regions is becoming blurred. The general public still maintains a fascination for exotic ornamental plants and companion animals from different countries. In addition, there is considerable interest within industry and government sectors in the deliberate introduction of non-native species for their usefulness as protein source (for human or livestock food) or biofuel production. Even some scientists (who should know better) exhibit enthusiasm regarding the irreversible ecological changes caused by non-native species and embrace these radically altered ecosystems as novel and inevitable. Yet, recent pest outbreaks and disease epidemics raise awareness of the threat posed by nonnative species.

Non-native species are increasingly a cause of conflict as one sector seeks to introduce species for economic benefit while another group argues against such action because of the potential for environmental harm. Even unintentionally introduced species can be simply viewed as a cost of improved trade that has to be seen against the economic benefits of accessing global markets. Resolving such conflicts are challenging even when the impact of biological invasions can be easily quantified in monetary terms. However, in most cases impacts are difficult to quantify in such simple terms because they affect aesthetics, sense of place, and the value of individual species.

These tangible and nontangible impacts can be framed under the ecosystem services approach. Ecosystem services can be defined as the goods that nature provides to people. The classification of ecosystem services encapsulates the different facets of biodiversity that influence people's lives and well-being. In this book, we used this approach as a guide to highlight the major impacts of the introduction of non-native species on our planet, which include impacts on supporting, provisioning, regulating, and cultural services. This framework allows us to integrate ecological and economic impacts and beyond because the consequences of the introduction of non-native species need to be examined broadly across taxa, across ecosystems, and across disciplines. We hope that this book helps to raise awareness about biological invasions as a human-driven change in the quality of life, and points towards solutions so that we can reap the benefits of non-native species without incurring their costs.

Sevilla, Spain
Lincoln, New Zealand
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Montserrat Vilà
Philip E. Hulme

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Chapter 1
Non-native Species, Ecosystem Services, and Human Well-Being

Montserrat Vilà and Philip E. Hulme

Abstract The management of biological invasions is necessary, not only to sustain biodiversity and the environment, but also to safeguard productive sectors. Non-native species, whether weeds in crops, pests in forests, or parasites in livestock, can heavily impact economic productivity in the agricultural, forestry, and fisheries sectors. Furthermore, many non-native species are vectors of human diseases and thus pose a serious threat to public health. In the last decade, there has also been increasing interest in the threat that some non-native species pose to social activities, such as leisure or ecotourism. Much of the focus of studies evaluating the impacts of the introduction and spread of non-native species has been on their effects on the environment, such as impacts on biodiversity and ecosystem properties, but translating these impacts into monetary value, especially when addressing cultural and aesthetic values, can be difficult. Yet independently of whether impacts fall most heavily on the environment, agriculture, or society, the costs of non-native species are incurred at every stage of the invasion process: from prevention and early warning, to control and local eradication, and to increased damage costs. In this book, we follow the Millennium Ecosystem Assessment framework to encapsulate the ecological and socioeconomic impacts of non-native species on a wide range of ecosystem services, thereby providing a comprehensive description of the impacts of non-native species from all five kingdoms of life across all categories of ecosystems.

Keywords Biodiversity • Cultural services • Human perception • Ecological engineers • Ecological impacts • Monetary costs • Provisioning services • Regulating services • Socioeconomy • Supporting services

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1.1 Why Focus on Ecosystem Services and Non-native Species?

Human well-being is intrinsically linked to the services provided by the ecosystems in which we live. In a healthy ecosystem, these functions form part of a balanced interplay that ensures the needs of all species within a habitat are met. However, global change, including the introduction and spread of non-native species, skews the balance of these services, often disrupting biodiversity with considerable negative consequences for human health and well-being.

It is well accepted that the introduction of non-native species causes both ecological and economic impacts on ecosystem services worldwide through their impacts on biodiversity and ecosystem processes (Simberloff et al. 2013). Nevertheless, only recently has the quantification of the impacts of non-native species on ecosystem services become an important research area in invasion biology. Research to quantify these impacts ideally needs to have a dual focus that investigates both the ecological and economic impacts of each non-native species and for each of the four types of ecosystem service (i.e., supporting, provisioning, regulating, and cultural services) (Fig. 1.1).

Historically, ecological research has mainly focused on changes in biodiversity after invasion, largely in relationship to decreases in species richness and abundance (Vilà et al. 2011, 2015; Gallardo et al. 2016; Cameron et al. 2016), with little attention directed towards the impacts on specific ecosystem services (Fig. 1.1). Attempts to adequately quantify the impact of non-native species have tended to take a broad brush to ecosystem services, treating each relatively lightly (Charles and Dukes 2007; Pejchar and Mooney 2009; Vilà et al. 2010), or have focused on a particular non-native species taxon, habitat, or ecosystem service (Katsanevakis et al. 2014). This research focus has changed in the past decade to include consideration of the impacts on other ecosystem processes, such as nutrient and water cycling (supporting services), and the alteration of disturbance processes, mainly erosion rates or fire regimes (regulating services; Ehrenfeld 2003). Impacts on regulating services, particularly water regulation or the vectoring of human diseases, tend to be somewhat less well studied but are often still quantified. The impacts on cultural services and human well-being, although often well publicised (e.g., algal blooms in coastal areas), present the greatest challenge for valuation, and this is reflected in a paucity of research in this area until recently.

Not surprisingly, current knowledge is strongly biased towards services that have marketable values. Research with an economic focus tends to consider the impact of a non-native species on provisioning services and primarily examines the effects of invasions on agricultural, forestry, and human health sectors (Pimentel et al. 2005; Colautti et al. 2006; Lovell et al. 2006). Much of the reported impacts on provisioning services comes from agricultural sectors (e.g., pest control), reflecting their economic importance, with the impacts easily quantified in monetary terms and with data often widely available. Most of the available data on supporting services also come from agricultural environments, where non-native species may alter C sequestration or soil erosion, again because of the economic factors involved in

SUPPORTING

Changes in primary production and C sequestration (*Elodea canadensis*, New Zealand lakes)
Modification of habitat quality (*Lumbricus terrestris,* Canadian forests)
Alteration of nitrogen cycling (*Acacia longifolia,* Portuguese coastal dunes)
Hydrological impacts (*Castor canadensis,* Chilean rivers)

PROVISIONING

Decrease in crop production (*Cirsium arvense,* N American cereal crops)
Impacts on forestry (*Lymantria dispar*, USA broadleaved trees)
Interference with aquaculture and fisheries (*Siganus luridus*, Eastern Mediterranean Sea)
Impacts on livestock (Bluetongue virus –BTV-, European ruminants)

REGULATING

Local extinction of endemic species (*Lates niloticus*, Tanzanian lakes)
Infectious diseases in wildlife (Rinderpest virus, African antilopes)
Non-target effects of biological control (*Larinus planus,* USA grasslands)
Disruption of pollination services (*Bombus terrestris,* Argentina)
Alteration of water quality (*Chryrosporum ovalisporum,* Portuguese lakes)
Damage to infrastructures (*Dreissena polymorpha*, USA lakes)
Alteration of disturbance regimes (*Sus scrofa*, USA shrublands)

CULTURAL AND HUMAN WELL-BEING

Spread of vectored diseases (Chikungunya virus by *Aedes albopictus,* Caribbean)
Impacts of toxins, allergenic substances and injuries (*Ambrosia artemisifolia,* Germany)
Conflicts with poverty alleviation (*Pomacea canaliculata*, Philippines)
Perception of nature and aesthetics (*Acacia* spp., world)

Fig. 1.1 Examples of the major impacts of biological invasions on the four main types of ecosystem services, which are (*1*) supporting services, the essential ecosystem processes needed to sustain life on Earth that provide the habitat characteristics to the biota; (*2*) provisioning services, the main biological assets humans need to provide food, fibre, and fuel; (*3*) regulating services, those needed to adjust and sustain the ecological conditions for living; and (*4*) cultural services, describing the influence of the biotic and abiotic components of ecosystems on human health and well-being, including psychological and social values

any disruptions caused by invasive species. It is now time to focus on the impacts on marketable and nonmarketable values of ecosystem services in a more balanced way (Egoh et al. 2007).

1.2 An Integrated View of Non-native Species Impacts on Ecosystem Services

The Millennium Ecosystem Assessment (MEA 2005) was established in 2001 to address a different approach to the conservation of biological diversity and to assess the consequences of changes in ecosystems for human well-being. It called for scientific investigation into the actions required to enhance the conservation and sustainable use of ecosystems globally. The predominance of this approach in many fields of knowledge has set a timely framework to place the impacts of biological invasions into a broad perspective. A few attempts have already been made to apply the MEA framework to the field of biological invasions (Binimelis et al. 2007; Charles and Dukes 2007; Pejchar and Mooney 2009; Boyd et al. 2013), yet an integrated and comprehensive view across taxa, ecosystems, and regions is still lacking.

The present book aims to be a departure from these norms by attempting to give the broadest possible overview of non-native impacts on ecosystem services. Here, we follow the MEA framework to encapsulate the ecological and socioeconomic impacts of non-native species on ecosystem services, thereby providing a comprehensive description of the impacts of non-native species from all five kingdoms of life across all ecosystem types on ecosystem services. This chapter provides an introductory overview of the current knowledge of the impacts on each of the four ecosystem services and evaluates the existing synergies and conflicts between them. All these impacts are described and discussed at length in the chapters of this book.

1.2.1 Impacts on Supporting Services

Supporting services are the basis for nutrient and energy flows. There are three main components that contribute to these flows, including primary productivity, nutrient and water cycling, and habitat structure. Biological invasions can impact each of these components within the supporting services, as illustrated in a seminal study by Vitousek and Walker (1989) showing the dramatic impact a non-native plant can have on N soil cycling. Some plants have mutualistic N_2-fixing microorganisms; thus, the N obtained through this mechanism first accumulates in the plant tissue, but rapidly cycles within the ecosystem and then accumulates in the soil. Major changes can occur in the fertility of the soil when a N_2-fixing species is introduced in a poor soil. Vitousek and Walker (1989) demonstrated that the introduction of the Macaronesian actinorhizal N_2-fixing shrub, *Morella faya*, into Hawaii by Portuguese settlers in the late 1800s, increased soil N by one order of magnitude after it soon spread to young lava flows and open-canopy forests. The lack of native N_2-fixers in these early-succession ecosystems enhanced N mineralization, thereby contributing to the increasing soil N. Since this pioneering work, there have been dozens of studies showing changes in N cycling after invasion (Castro-Diez and Alonso 2017). Many of these changes are irreversible and change the habitat conditions for both plant and animal native species.

Some non-native species affecting supporting services behave as ecological engineers that significantly modify or destroy the habitat suitable for native species: for instance, the impact on water flow and sedimentation produced by the establishment of non-native aquatic mammals, such as beavers and coypus, or the alteration of the morphology and hydraulics of waterways by the expansion of submerged and floating non-native macrophytes (Catford 2017). Non-native macrophytes also cause major changes in the primary productivity and C cycling of the invaded aquatic ecosystems (Nie et al. 2017). Other examples of impacts on primary productivity are the plantation and spread of fast-growing trees. Major impacts on supporting services occur by changes in habitat quality, such as those caused by the spread of non-native reef-forming organisms (e.g., introduced oysters, tube worms, mussels) that modify the whole trophic structure of the community (Gutierrez 2017).

1.2.2 Impacts on Provisioning Services

Biological invasions are increasingly important in national economies as they reduce the quality and quantity of products obtained from ecosystems. The production of consumable goods as part of a provisioning service is the most tangible ecosystem service and the easiest to quantify economically. Costs can be incurred through weeds, pests, and pathogens that reduce crop and timber production both in the field and during storage or shipment (Fried et al. 2017). Similarly, non-native species can reduce fisheries yields through competition, predation, and diseases, or by interfering with the process of fishing itself by fouling fishing equipment (Gozlan 2017). Livestock production can also be reduced, not only by diseases transmitted by non-native vectors such as ticks, but also by toxic non-native plants that reduce the quality of pastures (French 2017). In agricultural and sylvicultural systems, it is often quite simple to model yield losses into monetary costs, and to scale these values from the plot level to the regional level. Agricultural and forestry sciences have developed methods that also include costs of management associated with these productivity losses (Kenis et al. 2017). However, production systems are often the source of many non-native species such as North American pines in South Africa, Mozambique tilapia in Asia, American mink in Europe, and European rabbits in Australasia. The economic impacts of these non-native species are less often quantified.

1.2.3 Impacts on Regulating Services

Species interactions that disrupt the basic properties of ecosystems, from the lowest to the highest level of complexity, are at the heart of regulating services. Many biological invasions affect this ecosystem service by altering local food webs as well as populations of native species and the landscapes they occupy.

One of the most studied impacts in this category is the displacement and local extinction of native and endemic species, especially on islands (Pyšek et al. 2017). The cascading effects of introduced predators or omnivores on islands have received a fair amount of attention: examples include the introduction of crayfish and carp in many aquatic ecosystems of the world (Jones et al. 2016).

In the past decade, there has been great emphasis on the impact of biological invasions on host–parasite interactions and on mutualistic plant–animal interactions (Morand 2017). Many introduced species are vectors of diseases affecting wildlife (e.g., the chytrid fungus, *Batrachochytrium dendrobatidis*, on amphibians), a phenomenon that is being exacerbated by habitat destruction and climate change. In some cases it has been the introduced biological control agents that have spilled over to non-target native species that have caused conservation concern (Myers and Cory 2017), whereas the most studied animal–plant interaction has been the disruption caused by introduced non-native pollinators and flowering plants to the pollination services to wild plants and crops (Morales et al. 2017).

Non-native species can also cause major abiotic impacts, for instance, the regulation of water quality. The toxicity and pollution of marine waters by non-native microorganisms, such as diatoms and dinoflagellate algae, are examples of this sort, with negative consequences for the native biota, nutrient cycling, and human health (Costa et al. 2017).

At a large spatial scale, the presence and activity of non-native species can interfere with the regulation of disturbance regimes (Gaertner et al. 2017). One of the most studied impacts of this type is the effect of flammable non-native plants on fire risk and fire regimes. Finally, invasions can also damage the infrastructures constructed to regulate transport corridors, energy flow, or watercourses (e.g., pipes, maritime docks, traffic corridors, fences, buildings) by fouling these structures and reducing their effectiveness (Booy et al. 2017).

1.2.4 Impacts on Cultural Services and Human Well-Being

Some non-native species pose a hazard to human health (Mazza et al. 2014; Rabitsch et al. 2017; Nentwig et al. 2017). The most obvious cases include vectors of human diseases, such as the tiger mosquito, *Aedes albopictus*. Some can also cause injuries, toxicity, and allergies (e.g., pollen). Another human dimension, which is highly relevant to public health, relates to the extent to which the introduction of non-native species, especially in developing countries, has increased or decreased the standards of human well-being. Many non-native species have been extensively planted as monocultures or intensively produced in aquaculture for economic benefit. In many cases, these productive activities have provided new jobs, but in doing so they have displaced traditional knowledge and, often, have not alleviated poverty (Witt 2017).

We also need to preserve the non-material benefits of ecosystems. The recreational and aesthetic values of ecosystems are extremely important to us, not only to preserve our sense of place and cultural identity, but also from a productive perspective (Kueffer and Kull 2017). Ecotourism and the safeguard of sacred species and sites are somehow based on these values, yet we still often choose to introduce many non-native species as a result of curiosity, aesthetics, or fashion (e.g., ornamental plants, pets, game species). The aesthetic perceptions of biological invasions therefore seem ambivalent and warrant critical examination.

We recognise that biological invasions have a strong human component and that their valuation can be on subjective assets, such as species aesthetics or the educational value of ecosystems (Tassin and Kull 2015). Sense of place is a cultural service that can be modified by the presence of non-native species. For example, in rural, semiarid lands in Southern Spain, several South American desert plants, such as *Agave* spp., were planted first as ornamentals and later, in the 1950s, over large expanses for fibre production. However, this was never intended to be a significant economic activity. Currently, *Agave* spp. are widespread in the Cabo de Gata Natural Park landscape, competing with many endemic steppe species and threatening EU priority habitats for conservation (Fig. 1.2). Pictures of *Agave* at sunset are common on postcards and brochures targeted at people looking for an "exotic" Mediterranean tourist destination. Thus, even if eradication of the species is feasible, some conservationist groups oppose such action, claiming that the species has a symbolic value and is part of the identity and historical legacy of the area.

Fig. 1.2 Image of an invaded landscape with *Agave* spp. in Cabo de Gata Natutral Park (Andalucía, Spain) (Photograph by Montserrat Vilà)

1.3 Synergies Among Impacts on Ecosystem Services

Ecosystem services are interrelated in complex ways. Thus, many non-native species can cause disruptions to several ecosystem service types simultaneously or through cascading effects. Using a list of 100 of the worst non-native species in Europe (DAISIE 2009), we found that although less than 8 % of the species are known to cause impacts on a single ecosystem service category, most invasive species cause impacts to several categories of ecosystem services (Vilà et al. 2010). We examined the pairwise association between each of the four ecosystem services categories affected by these 100 non-native species (Fig. 1.3). Regulating and provisioning services are strongly linked to each other as well as to the other two ecosystem service categories. The weakest links are between cultural services and either regulating or supporting services. These trends need to be interpreted with caution because they may simply reflect that regulating and provisioning services are more easily measured and often using similar methods, whereas assessments of cultural services often require a multidisciplinary approach that may be less frequently adopted. Nevertheless, these associations among impacts are the reason why many of the more than 500 species described in this book appear several times across chapters.

There are significant differences between taxonomic groups and the number of impacts they inflict when all the subcategories of ecosystem services are considered (indicated in Fig. 1.1). Terrestrial vertebrates exhibit the widest range of impact on ecosystem services (Vilà et al. 2010). Taking the coypu, *Myocastor* coypu, as an example, this large rodent introduced from South America to Europe modifies habitat quality by undermining riverbanks (supporting service), damages crops

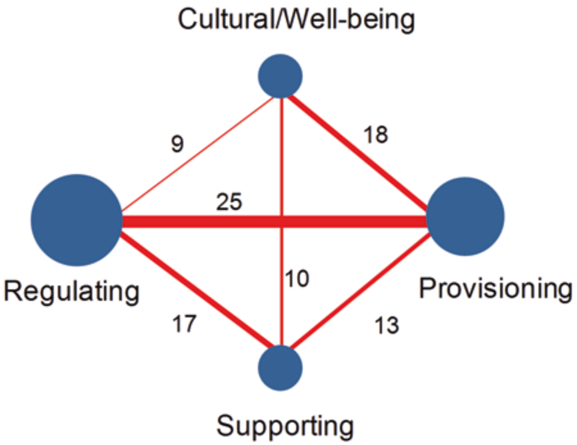

Fig. 1.3 Percentage of links between impacts on ecosystem services for 100 of the worst invasive species in Europe. The size of the nodes reflects the number of species having an impact on them, and the width of the connecting lines represents the strength of the association between pairs of impacts on ecosystem services. The network analysis was conducted with R packages *network* (Butts 2015) and *ggplot2* (Wickham 2009)

(provisioning service), disturbs riverine vegetation and even damages infrastructures (regulating service), as well as transmitting leptospirosis disease (human well-being).

Similarly, invasion by feral pigs, *Sus scrofa,* and goats, *Capra aegagrus hircus*, have caused cascading effects on ecosystem services, particularly on islands (Peh et al. 2015). In the forests of Montserrat in the Caribbean, feral populations of these ungulates disturb the soil (regulating service), leading to the replacement of the native vegetation with the non-native guava, *Psidium guajava,* and the Java plum, *Syzgium cumini*, which are dispersed by pigs. These changes in the forest understory alter the nesting habitat of the endangered endemic guava, *Psidium guajava,* (supporting service), which is one of the attractions for nature-based tourism of the island (cultural service). Cessation of the control program of feral livestock will not only reduce 46 % of bird-watching tourism but also 36 % in harvested wild meat (provisioning service). The benefits of controlling these feral ungulates have been estimated to be US$214.000/year (Peh et al. 2015).

Some of the indirect impacts on ecosystem services might well go unnoticed, including changes in human activities in response to the presence and nuisance of non-native species. However, few examples of this sort exist, most probably because they have been unexplored. The emerald ash borer, *Agrilus planipennis,* has devastated ash, *Fraxinus* spp., forests in midwest and northeast USA. A recent study has surveyed the leisure–labour time spent by the public across 469 counties in 22 USA states where the ash borer has been detected during the past 10 years (Jones 2016). The survey found that the public spent less time in outdoor activities and more time in labour activities when the pest is detected in their area, even before the impacts on trees are observed. The causes of this change in human behaviour are not known, but the study highlights the effect that the presence of this non-native insect has on well-being.

1.4 Conflict Among Impacts on Ecosystem Services

The role of potential conflict is a further issue relating to the impact of non-native species on ecosystem services. Some non-native plant and animal species provide benefits to humans in the form of food, fibre, fuel, and timber. Yet many of these useful species, should they escape from agricultural, forestry, or farming systems, may impact other supporting and regulating ecosystem services, such as nutrient cycling, water regulation, or soil conservation. This duality among many non-native species makes their net contribution to ecosystem services a challenge to quantify. To date, most attempts to quantify the impact of non-native species on human well-being have focused on monetary economic estimates (Colautti et al. 2006; Pimentel et al. 2005). Dimensions that go beyond monetary costs and benefits have yet to be explored in detail, but these might include the number of people affected positively or negatively by a particular non-native species and the magnitude of this impact on their lives (Pejchar and Mooney 2009). Indeed, it may become apparent that some sectors of society reap all the benefits while other sectors bear the costs.

Conflicting values are commonly found for non-native trees (Dickie et al. 2014). For example, non-native pines can be seen as positive because they increase forest primary production and provide wood, yet invasion by non-native pines can completely transform the landscape, change nutrient cycling, and reduce the availability of water for human use. Similarly, the value of introduced *Acacia* spp. swings from positive to negative depending on its commercial importance or environmental effects. The perception of these values in different countries is modulated by economic and political contexts (Carruthers et al. 2011; Kull et al. 2011).

Even the introduction of non-native species that are deemed to be highly positive economically can be considered negative when other aspects are explored in detail. In the past decade, *Tilapia* spp. farming has been one of the fastest growing global aquaculture industries. It has been introduced in at least 140 countries, and more than half these countries have reported feral populations. Although *Tilapia* spp. production serves one of the most buoyant markets in the aquaculture sector worldwide, environmental impacts are reported almost everywhere it has been studied (Deiners et al. 2016). Invasion by *Tilapia* spp. has decreased water quality and native populations of fishes, with important implications for the health of local people and their recreational or economic use of this resource. Despite the fact that this cannot be valued in monetary terms, there is the perception that the negative impacts are larger than the benefits and that these impacts are independent of the tilapia species considered and the region they occupy (Deiners et al. 2016).

Policies on invasive species often encounter social conflict when non-native species are first introduced for productive purposes. The Louisiana crayfish, *Procambarus clarkii,* is considered one of the worst non-native species in Europe and is listed as such in many countries of the world. Ecological impacts include predation on and competition with a variety of aquatic species, such as macrophytes, invertebrates, and amphibians; degradation of riverbanks and alteration of water quality because of its burrowing activity; and introduction of the crayfish plague, *Aphanomyces astaci*. It can cause significant economic impacts on irrigation structures, such as reservoirs, channels, or rice fields. Moreover, it accumulates heavy metals and toxins produced by cyanobacteria, such as *Microcystis aeruginosa*, and can transfer them to its consumers, including humans. It is an intermediate host of trematodes of the genus *Paragonimus*, which are potential pathogens of humans if undercooked crayfish are consumed. In the 1970s, 500 kg of Louisiana crayfish was introduced in the Guadalquivir marshes of Spain for aquaculture. Currently, 3–4 tonnes per year are fished and processed in the crab fishery industry of the area; 85 % of the production is exported, with Spain being the world's second largest producer. Based on scientific evidence of multiple environmental impacts, the Spanish Supreme Court wants to list the species as invasive in the Spanish Regulation on Invasive Species (Real Decreto 630/2013), thus reinforcing Louisiana crayfish control rather than its commercialisation. However, banning Louisiana crayfish fishing would collapse a local food industry and increase local unemployment, so this argu-

Table 1.1 Percentage of harmful non-native organisms regulated in eight countries according to their impact

	Australia	Japan	New Zealand	South Africa	Spain	Switzerland	UK	USA
	(1.275)	(1.334)	(14.831)	(886)	(546)	(371)	(546)	(1.331)
Biodiversity	73.6	23.8	4.4	89.4	54.8	47.2	41.0	35.2
Human health	7.9	5.0	1.0	10.5	11.2	10.0	9.0	5.0
Livelihood[a]	55.5	88.8	98.6	52.1	79.3	90.6	70.1	92.5

The total number of taxa per country is indicated in parentheses (Data extracted from García de Lomas and Vilà 2015)

Percentages within a country might be larger than 100 because some species cause various impacts

[a] Livelihood refers to losses in agriculture, livestock, forestry production, and fisheries as well as impacts on infrastructures

ment is used politically against the regulation of this highly invasive species. Policy regarding biological invasions confronts complex interrelated issues and needs to be collaborative and cross-sectorial. Policy has to integrate the management of non-native species while still considering all their impacts on ecosystem services (Hulme and Vilà 2017).

Clearly, policy-based responses are limited in their ability to mitigate the impacts of biological invasions. These policies are usually intended to control the dispersal of non-native species and are based on impacts on biodiversity, livelihoods, and human health (Table 1.1). However, the policies addressing the introduction, trade, use, tenure, quarantine, and elimination of non-native species are usually developed separately by environmental, food, and health administrative departments (Hulme 2011; García de Lomas and Vilà 2015), and the lack of coordination between the departments often makes it difficult to manage the impacts of biological invasions in a concerted way.

1.5 Conclusions

Biological invasions can modify all ecosystem services, some of which are difficult to value economically because of their intangible nature. The impact of a particular non-native species is rarely restricted to a single ecosystem service; rather, it might have cascading effects on several ecosystem services, and these effects can be irreversible. Nevertheless, it is premature to offer a global quantitative assessment of the impacts of biological invasions on ecosystem services, or even to identify which non-native taxa cause the greatest harm or which ecosystem services are more vulnerable to invasions. These evaluations are highly subject to human perceptions and conflicting interests among socioeconomic sectors. Therefore, interdisciplinary collaboration is needed to manage biological invasions to preserve environmental, economic, and societal values. Indeed, there is now an urgent need to engage both the private and the public sectors to manage biological invasions from an integrated perspective, not only for biodiversity conservation but also to preserve all the goods that nature provides to humanity (Funk et al. 2014). This book aims to catalyse such an inclusive perspective. Each chapter has been kept deliberately short and aims at representativeness rather than comprehensiveness because we want to encourage readers to explore the diversity of ecosystem impacts attributable to non-native species by reading multiple chapters. Those readers who want more depth in any one topic will find the key references to guide their quest, but the advances in our discipline will be made by those who can see the parallels across taxa, across biomes, and across ecosystem services.

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Part I
Impacts on Supporting Services

Chapter 2
Changes in Primary Production and Carbon Sequestration after Plant Invasions

Ming Nie, Lei Shang, Chengzhang Liao, and Bo Li

Abstract The potential differences in ecophysiological traits between native and invasive plants can change ecosystem functioning. In this chapter, we discuss the effects of plant invasions on ecosystem carbon (C) cycling in both terrestrial and aquatic ecosystems. In general, plant invasions increase ecosystem C fluxes and pool sizes. Most experiments testing plant invasion effects on C cycling have focused primarily on plant aboveground production and its associated processes, especially in terrestrial ecosystems. The impacts of plant invasions on belowground C cycling are relatively poorly understood, especially belowground C decomposition and the associated root effects and microbial processes. In addition, most experiments have been conducted to examine the effects of plant invasions on C sequestration in laboratory or small-scale field conditions, whereas ecosystem-scale experiments are underrepresented. This chapter highlights the need for multifactorial experimental approaches to understanding invasion-induced changes in ecosystem C processes in the context of multiple global environmental changes. The combination of experimental and modelling studies will help to predict feedbacks between plant invasions and ecosystem C cycling in a changing world.

Keywords Carbon cycling • Global environmental change • Photosynthesis • Plant ecophysiological traits • Primary production • Soil respiration

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2.1 Introduction

As ecosystem producers, plants have important roles in primary production and C sequestration. The ecosystem functions associated with C cycling are major factors in the ecosystem–atmosphere exchange of C and the ecosystem C budget (Le Quéré et al. 2015). At the global scale, plants are critical regulators of climate as they fix most of the released anthropogenic CO_2 from fossil fuel burning (Le Quéré et al. 2015). Furthermore, plant tissues are the main source of soil organic matter, which secures soil functionality and soil fertility (Schmidt et al. 2011). However, some invasive plants have traits such as high photosynthetic rate or rapid growth that allow them to replace native plants. Plant community composition altered by invasions can potentially change the primary production and C sequestration of invaded ecosystems (Ehrenfeld 2010). Therefore, understanding the effects of plant invasions on C cycling is one of the most important issues to be addressed to understand how ecosystem services can be maintained in a rapidly changing world.

During the past decade, many published studies suggest ecosystem C fluxes, such as plant photosynthesis, net primary production (NPP), soil respiration, and net ecosystem exchange (NEE), can be altered by plant invasions, which may eventually lead to changes in plant and soil C pool sizes. Recent meta-analyses suggest that invasive plants can accelerate ecosystem C cycling in terrestrial ecosystems (Liao et al. 2008; Cavaleri and Sack 2010; Davidson et al. 2011).

Aquatic ecosystems are also invaded by non-native plants. For example, 96 aquatic species from 30 families have been identified as introduced in a single European country (Hussner 2012). In contrast to relatively stable terrestrial ecosystems, the effects of plant invasions on C fluxes and pools are less well defined in aquatic ecosystems, which are dynamic and are characterized by moving water-driven interactions between aquatic organisms and their physical and chemical environments. Aquatic invasive plants can also greatly increase plant biomass and thus ecosystem C cycling in similar ways to terrestrial invasive plants (Ehrenfeld 2010). For example, invasive plants such as *Hydrocotyle ranunculoides* can cover the entire water surface and convert intact ecosystems of low production to invaded ecosystems of high production (Hussner 2009). In a New Zealand lake, plant beds invaded by the macrophytes *Lagarosiphon major* and *Elodea canadensis* (Hydrocharitaceae) have threefold greater plant biomass and twofold greater plant surface than those of native species (Kelly and Hawes 2005).

This chapter examines the impacts of plant invasions on ecosystem primary production and C sequestration in both terrestrial and aquatic ecosystems. The C processes (e.g., NPP and soil respiration) that mediate these two ecosystem functions are also discussed. The ecophysiological and phenological traits of invasive plants that influence primary production are also described along with future research prospects of plant invasion effects on ecosystem C cycling in a changing world.

2.2 Altered Ecosystem Carbon Cycling by Plant Invasions

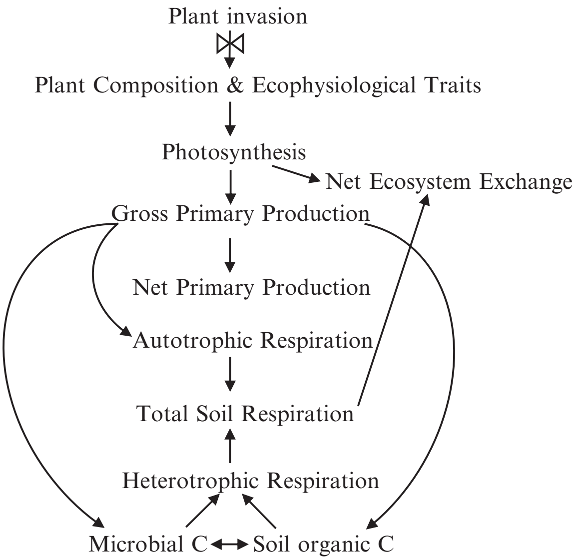
Plant invasions can influence interrelated ecosystem C processes through altering plant species composition and dominant ecophysiological traits of the invaded ecosystems (Fig. 2.1). These pathways are discussed separately next.

2.2.1 Primary Production

Primary production represents the major input of C and energy into the ecosystems on which almost all life on earth depends. Our meta-analysis, across a broad range of ecosystems including wetlands, has revealed that, in general, there is an increase in primary production with invasions, including increases in aboveground NPP (ANPP, +83 %) and litter production (+49 %), which correspondingly increase plant aboveground (+133 %) and belowground C pool sizes (+6 %) (Liao et al. 2008). The increase in ANPP with invasions varies across ecosystems: it can enhance ANPP by 79 % in forest and grassland ecosystems, and by twofold in wetland ecosystems (Liao et al. 2008).

The photosynthetic rate reflects the potential for plant biomass accumulation and ecosystem primary production. Through photosynthesis, plants transform C from atmospheric CO_2 into C-containing organic compounds (e.g., sugars) and drive whole-ecosystem C cycling. Ecosystem GPP and NPP are positively correlated with photosynthetic rate. Here we list the main ecophysiological traits that may be involved in higher photosynthetic rates and growth in invasive plants in comparison with co-occurring native plants.

Fig. 2.1 The potential impacts of plant invasions on ecosystem C cycling



C_4 Photosynthetic Pathway Approximately 80 % of the most invasive weeds in the world possess the C_4 photosynthetic pathway (Sage and Monson 1999). In general, C_4 plants are more efficient in photosynthetic C fixation and are more tolerant to abiotic stresses than C_3 plants.

Higher Resource-Use Efficiency N and water are the essential resources that determine plant photosynthetic capacity and growth rate. Photosynthetic N-use efficiency (NUE) and water-use efficiency (WUE) are expressed as the amounts of C converted into sugars per unit leaf N and per unit water transpired during the photosynthetic process, respectively. In nutrient-poor environments, invasive plants are usually more efficient in photosynthetic N use than co-occurring native plants. For example, in Hawaii, by comparing 19 phylogenetically related pairs of invasive and native plant species from three habitats where light, water, or N availability is limited, Funk and Vitousek (2007) found that invasive plants have higher NUEs that couple with higher photosynthesis C fixation. In contrast, in nutrient-rich conditions, some invasive plants, such as *Cortaderia selloana*, do not appear to have a higher NUE than coexisting natives because invasive plants tend to have high N content to support their vigorous growth rates (Vourlitis and Kroon 2013). A high photosynthetic C fixation can lead to extended stomatal opening, resulting in water loss through the transpiration process. In a recent meta-analysis, data from 40 studies showed that invasive plants have greater stomatal conductance than co-occurring native species (Cavaleri and Sack 2010). However, their analysis also suggested that invasive plants are not more efficient in utilizing water than are native plants (Cavaleri and Sack 2010).

Efficient Resource Allocation Specific leaf area (SLA), the ratio of leaf area to dry mass, is an indicator of light capture surface area per unit investment in leaf biomass and is positively correlated with plant growth rate. By analyzing community-level and global-scale leaf trait data, Leishman et al. (2007) have found that invasive plants have significantly higher SLA than native plants, possibly resulting in a higher photosynthetic capacity per unit leaf mass of invasive plants. Invasive plants with higher SLA may also allocate a lower fraction of leaf N to cell walls, leaving more N for photosynthesis, as observed in the invasive *Ageratina adenophora* (Feng et al. 2009). On the other hand, invasive plants can have lower SLA than co-occurring native plants. For example, invasive *Spartina alterniflora* has a lower SLA than the co-occurring natives, *Phragmites australis* and *Scirpus mariqueter*, in the Yangtze estuary, although the invasive has much higher production rates and outcompetes the two natives (Jiang et al. 2009).

Plant biomass allocation also influences vegetation and ecosystem properties, ranging from individual plant growth to ecosystem C processes. Some invasive plants allocate a greater proportion of their biomass to leaves (e.g., leaves and primary lateral branches) than stems or roots, resulting in a higher rate of photosynthetic C assimilation in comparison with phylogenetically related native plants. For example, invasive populations of *Lythrum salicaria* in Central Europe have higher leaf weight ratio than native populations, which results in more vigorous growth (Bastlová and Květ 2002).

Longer Phenological Period Another trait that determines production is photosynthetic season length. Although some invasive plants have photosynthetic rates that are similar to those of co-occurring native plants, they may emerge sooner and senesce later. In a 3-year study of 30 invasive and 43 native plants in the eastern United States, for example, invasive plants were found to exhibit systematic differences in growth phenology, and have an average 4-week-longer autumn growing season compared with native plants (Fridley 2012). The phenological differences lead invasive plants to have a longer photosynthetic season than co-occurring native plants and considerably increase annual C gain in the invaded ecosystems (Leishman et al. 2007; Liao et al. 2007).

Lower Leaf Construction Cost Leaf construction requires energy to transport and assemble materials in the leaves. Construction cost (CC) is a quantifiable measurement of the amount of energy required for leaf biomass production, defined as the amount of photosynthetically fixed C used to construct a unit quantity of leaf tissue. In nutrient-poor environments, invasive plants may benefit from low CC, and thus save energy for leaf production. In a comparative study involving 83 populations of 34 native and 30 invasive plants across elevation and substrate age gradients in Hawaii, Baruch and Goldstein (1999) found that CC is lower in invasive plants than in native plants. This trait matches with the higher growth rates of the invasive plants. In an aquatic ecosystem, invasive *Lythrum salicaria* also exhibits the lowest CC compared with the most abundant co-occurring native plants (Nagel and Griffin 2001).

Higher Capacity of Light Acclimation Light is a factor limiting plant survival and growth, especially in closed-canopy forests. However, canopy gaps created by disturbances (e.g., typhoons, treefall) can suddenly increase light availability, possibly leading to a greater chance of seedling survival in plants that have high acclimation capacities. In a comparative study, the invasive tree *Bischofia javanica* and three native trees were grown under increased light availability. The seedlings of the former had the highest ability to increase their maximum photosynthetic rate of shade leaves, produce newly formed sun leaves, and increase their relative growth rate (Yamashita et al. 2000). These results suggest that the invasive tree has a greater ability to respond to changing light levels than the native trees (Yamashita et al. 2000).

Greater Phenotypic Plasticity Invasive plants with high phenotypic plasticity have the ability to change community structure and functioning under variable environmental conditions and increase their abilities to occupy more habitat types. In a synthetic study involving the data from 75 pairs of invasive/noninvasive plants, Davidson et al. (2011) have found that invasive plants have significantly higher phenotypic plasticity than native plants. Greater phenotypic plasticity of plant traits (e.g., root:shoot ratio) allows invasive plants to adapt to a wide range of resource availabilities and may facilitate them to successfully colonize new ranges.

2.2.2 Soil Respiration

Soil respiration is the process of CO_2 entering the atmosphere from the soil and is identified as the largest flux in terms of ecosystem C loss (Mauritz and Lipson 2013). Soil respiration is affected by plant C input to soil, as well as soil biotic and abiotic conditions. Plant invasions have the potential to influence the soil respiration rate by the changes of the biotic (e.g., plant root biomass, litter quantity and quality, soil microbial community structure, and functioning) and the abiotic (e.g., soil water availability through altering timing and depth of water acquisition, soil temperature by shade) environments (Liao et al. 2007, 2008; Ehrenfeld 2010; Bu et al. 2015). In most cases, plant invasions increase soil C decomposition and soil respiration rate (Table 2.1). Additionally, plant invasions are also documented to change the temperature sensitivity of soil respiration (Mauritz and Lipson 2013).

Total soil respiration can be divided into autotrophic and heterotrophic components, which are the respiratory products by plant roots and soil decomposers, respectively. Both components may change differentially with respect to invasion in ecosystem C cycling. Unfortunately, few studies have been conducted to address this issue. In semiarid shrublands, plant invasions greatly increase total soil respiration rate through stimulating soil autotrophic respiration, whereas plant invasions are found not to change cumulative soil heterotrophic respiration but do alter its seasonal pattern (Mauritz and Lipson 2013).

Aquatic ecosystems are the most important sources of atmospheric methane. Methane efflux through anaerobic respiration is one of the ecosystem C loss processes. Highly variable responses of methane emission to plant invasions have been observed in aquatic ecosystems. For example, *Spartina alterniflora* invasion can accelerate methane emission in a Chinese salt marsh (Yuan et al. 2014). In contrast, *Phalaris arundinacea* and *Typha angustifolia* have the lowest methane emissions of all nine studied species in a controlled greenhouse experiment (Kao-Kniffin et al. 2010). The differences in ability of oxygen transport to anoxic sediments, which can stimulate methane consumption by bacteria, contribute to these highly variable responses of methane emission to plant invasions in aquatic ecosystems.

2.2.3 Ecosystem Carbon Pools

Although plant invasions can significantly increase plant above- and belowground C pools, soil C pool, and microbial C pools, there is a high variability in the direction and magnitude of changes in C pool sizes among ecosystems (Liao et al. 2008). In grasslands, which tend to be invaded by woody species with higher biomass,

Table 2.1 Summary of selected case studies of the effects of plant invasions on main ecosystem C fluxes

Invaded ecosystem	Native species	Invasive species	Method	Invasion effect	Reference
Photosynthetic rate					
Rainforests	*Pipturus albidus*	*Schinus terebinthifolius*	Pacsys 9900 gas exchange system with an Li-Cor 6600 infrared gas analyzer	> +100 % (average light-saturated photosynthetic rates, grown in the sun)	(1) Pattison et al. (1998)
	Hedyotis terminalis	*Citharexylum caudatum*			
	Psychotria mariniana	*Cestrum nocturnum*			
	Bidens sandwicensis	*Psidium cattleianum*			
		Bidens pilosa			
Salt marshes	*Phragmites australis*	*Spartina alterniflora*	Li-Cor 6400	+16 % (maximal net photosynthetic rate)	(2) Jiang et al. (2009)
Salt marshes	*Scirpus mariqueter*	*Spartina alterniflora*	Li-Cor 6400	+121 % (maximal net photosynthetic rate)	(2) Jiang et al. (2009)
Forests and shrublands	*Acacia koa*	*Falcataria moluccana*	Li-Cor 6400	No significant change (mass-based net photosynthetic rate)	(3) Funk et al. (2013)
	Dodonaea viscosa	*Leucaena leucocephala*			
	Osteomeles anthyllidifolia	*Psidium cattleianum*			
	Pipturus albidus	*Pyracantha angustifolia*			
	Sophora chrysophylla	*Schinus terebinthifolius*			
Aboveground net primary production					
Grasslands	*Andropogon gerardii*	*Cornus drummondii*	Aboveground biomass conversion	+197 %	(4) Lett et al. (2004)

(continued)

Table 2.1 (continued)

Invaded ecosystem	Native species	Invasive species	Method	Invasion effect	Reference
	Sorghastrum nutans				
	Panicum virgatum				
Salt marshes	*Puccinellia maritima*	*Elymus athericus*	Aboveground biomass conversion	+51 %	(5) Valéry et al. (2004)
	Aster tripolium				
	Suaeda maritima				
	Atriplex portulacoides				
Grasslands	*Schizachyrium scoparium*	*Bothriochloa ischaemum*	Aboveground biomass conversion	+80 %	(6) Wilsey and Polley (2006)
	Sporobolus compositus	*Paspalum dilatatum*			
	Bothriochloa laguroides	*Panicum coloratum*			
	Bouteloua curtipendula				
	Sorghastrum nutans				
High-country lakes	*Isoetes alpinus*	*Elodea canadensis*	^{14}C technique	+41 % (epiphyton primary production); 10× greater (macrophyte primary production)	(7) Kelly and Hawes (2005)
	Potamogeton cheesemanii	*Lagarosiphon major*			
	Myriophyllum triphyllum				
Soil respiration					
Tropical dry forests	*Diospyrossandwicensis*	*Pennisetum setaceum*	LI-Cor 6400 system and ^{13}C isotope	+37 % to + 40 % (annual cumulative CO_2 efflux)	(8) Litton et al. (2008)
	Psydrax odorata				
Shrublands	*Artemisia californica*	*Centaurea solstitialis*	LI-8100 automated soil CO_2 flux system	+40 % (cumulative CO_2 efflux)	(9) Mauritz and Lipson (2013)

	Eriogonum fasciculatum	*Bromus madritensis*			
	Salvia mellifera	*Hirschfeldia incana*			
Grasslands	*Pseudoroegneriaspicata*	*Centaurea maculosa*	Soil incubation	+81 % (potentially respirable C)	(10) Hook et al. (2004)
	Festuca idahoensis				
	Pascopyron smithii				
	Stipa comata				
Shrublands	*Artemisia californica*	*Bromus madritensis*	Field respiration measurement	+18 % (annual cumulative CO_2 efflux)	(11) Wolkovich et al. (2010)
	Salvia mellifera	*Brachypodium distachyon*			
Freshwater lakes	*Sagittaria latifolia*	*Phragmites australis*	Soil incubation	+78 % (basal respiration)	(12) Rothman and Bouchard (2007)

References: (1) Pattison RR, Goldstein G, Ares A (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia (Berl) 117:449–459; (2) Jiang LF, Luo YQ, Chen JK et al. (2009) Ecophysiological characteristics of invasive *Spartina alterniflora* and native species in salt marshes of Yangtze River estuary, China. Estuar Coast Shelf Sci 81:74–82; (3) Funk JL, Glenwinkel LA, Sack L (2013) Differential allocation to photosynthetic and non-photosynthetic nitrogen fractions among native and invasive species. Plos One 8:e64502; (4) Lett MS, Knapp AK, Briggs JM et al. (2004) Influence of shrub encroachment on aboveground net primary productivity and carbon and nitrogen pools in a mesic grassland. Can J Plant Sci 82:1363–1370; (5) Valéry L, Bouchard V, Lefeuvre J (2004) Impact of the invasive native species *Elymus athericus* on carbon pools in a salt marsh. Wetlands 24:268–276; (6) Wilsey BJ, Polley HW (2006) Aboveground productivity and root–shoot allocation differ between native and introduced grass species. Oecologia (Berl) 150:300–309; (7) Kelly DJ, Hawes I (2005) Effects of invasive macrophytes on littoral-zone productivity and foodweb dynamics in a New Zealand high-country lake. J N Am Benthol Soc 24:300–320; (8) Litton CM, Sandquist DR, Cordell S (2008) A non-native invasive grass increases soil carbon flux in a Hawaiian tropical dry forest. Global Change Biol 14:726–739; (9) Mauritz M, Lipson D (2013) Altered phenology and temperature sensitivity of invasive annual grasses and forbs changes autotrophic and heterotrophic respiration rates in a semi-arid shrub community. Biogeosci Disc 10:6335–6375; (10) Hook PB, Olson BE, Wraith JM (2004) Effects of the invasive forb *Centaurea maculosa* on grassland carbon and nitrogen pools in Montana, USA. Ecosystems 7:686–694; (11) Wolkovich EM, Lipson DA, Virginia RA et al. (2010) Grass invasion causes rapid increases in ecosystem carbon and nitrogen storage in a semiarid shrubland. Global Change Biol 16:1351–1365; (12) Rothman E, Bouchard V (2007) Regulation of carbon processes by macrophyte species in a Great Lakes coastal wetland. Wetlands 27:1134–1143 plant invasions increase the pool sizes of plant aboveground C (+70 %), litter C (+31 %), soil C (+4 %), and microbial C (+77 %). Plant invasions slightly decrease grassland plant belowground C pool size by 4 % on average. In wetlands, plant invasions increase the pool sizes of plant aboveground and belowground C (+210 % and +57 %, respectively), litter C (+72 %), and soil C (+7 %). Microbial C pool size appears not to significantly respond to plant invasions in wetlands. In forest ecosystems, plant invasions respectively increase litter and soil C pool sizes by +92 % and +9 % on average. In contrast, plant invasions decrease the pool sizes of plant above- and belowground C (−54 % and −74 %, respectively) and microbial C (−11 %) in forest ecosystems. Unfortunately, the knowledge of soil C dynamics and its associated plant–soil processes/physical environments in invaded ecosystems is still limited, which precludes us from generalizing how soil C sequestration is altered in response to plant invasion. Because ecosystem C sequestration is a long-term process of C storage, more long-term measurements and model evaluation of plant invasion impacts on ecosystem C dynamics would be very useful to improve our understanding of ecosystem C sequestration.

2.2.4 Net Ecosystem Exchange

The net C exchange between an ecosystem and the atmosphere quantifies how much C is gained and lost in an ecosystem. Few attempts have been made to explore this process in the context of plant invasions. In the eastern salt marshes of China, for instance, *Spartina alterniflora* invasion increases ecosystem C sequestration (Zhou et al. 2014). In contrast, decreased C sequestration in sagebrush communities invaded by annual grasses is also observed, which may cause positive feedback to affect climate change (Prater et al. 2006). Therefore, further research is urgently needed to quantify net ecosystem exchange in invaded ecosystems for understanding how plant invasions contribute to land–atmosphere C exchange, especially in the ecosystem-level experiments.

2.3 A Case Study: *Spartina alterniflora* Invasion in Salt Marshes of Yangtze Estuary, China

Spartina alterniflora is a global C_4 invader in coastal wetlands with multiple consequences for the invaded nearshore ecosystems. Its invasion results in reduced ranges of native plants and alters plant community structure and functioning (Fig. 2.2). *Spartina alterniflora* generally causes an increase of primary production in salt marsh ecosystems of the Yangtze estuary. Aboveground production of invasive *S. alterniflora* marshlands is much greater than that of native *Scirpus mariqueter* and *Phragmites australis* marshlands, resulting from the invader's longer growing

Fig. 2.2 'Tall' nonnative *Spartina alterniflora* is invading and replacing 'short' native *Scirpus mariqueter* monocultures at Chongming Dongtan wetland in the Yangtze estuary, China

season, higher leaf area index, and higher photosynthetic rate (Liao et al. 2007; Jiang et al. 2009). Therefore, *S. alterniflora* produces a larger amount of litter than the natives, although the litter decomposition rate is generally lower than those of *S. mariqueter* and *P. australis* because of its lower quality (Liao et al. 2008). *Spartina alterniflora* has relatively lower N concentrations of leaf and root (1.4 % and 0.7 %, respectively) compared to those of native *P. australis* (1.5 % and 0.8 % for leaf and root respectively, hereafter) and *S. mariqueter* (1.55 % and 1.13 %) (Liao et al. 2008). Mean annual size of total plant C pool (i.e., aboveground plus belowground) in *Spartina* marshlands is estimated to be 3.0 kg m^{-2}, which is 2.5 and 0.7 kg m^{-2} greater than that in *S. mariqueter* and *P. australis* marshlands, respectively (Liao et al. 2007).

Similarly, soil C pool size in salt marsh ecosystems can be enhanced by *S. alterniflora* invasion (Liao et al. 2007). As the key component of the soil C pool, soil organic carbon is observed to be greater in *S. alterniflora*-invaded marshlands than in native ones (Bu et al. 2015). Thus, its invasion can affect soil C cycling and other related ecosystem processes through altering the quantity and quality of soil organic carbon. In addition, microbial C pool size is observed to increase after the invasion (Bu et al. 2015), which is partially attributed to the higher plant C input of *S. alterniflora* than that of native grasses (Liao et al. 2007; Bu et al. 2015). Mean soil respiration rates are 185.8 and 142.3 mg CO_2 m^{-2} h^{-1}, respectively, in invasive *S. alterniflora* and native *P. australis* marshlands in the higher tidal zone, and 159.7 and 112.0 mg CO_2 m^{-2} h^{-1}, respectively, in invasive *S. alterniflora* and *S. mariqueter* marshlands in the lower tidal zone. Because enhanced production by *S. alterniflora* exceeds invasion-induced C loss through soil respiration, its invasion might strengthen ecosystem C sequestration in the Yangtze estuary (Bu et al. 2015).

2.4 Conclusions

It is clear that plant invasions can alter primary production and C sequestration to varying degrees, consequently changing the supporting and regulating services of invaded ecosystems. To date, most of the existing studies have examined the community- and population-level effects, but ecosystem-level approaches are obviously required to better understand the roles of invasive plants in global C cycling. Addressing this challenge requires a collaborative network to link flux measurements at the whole-ecosystem scale to modeling predictions. Belowground processes in the invaded ecosystems are even less well understood. We do not fully understand how root effects, microbial functions, and their interactions respond to plant invasions, which may preclude us from understanding how invasive plants affect ecosystem C exchange.

Another challenge is to understand how plant invasions interact with climate change, land use change, and other environmental changes. Climate change can promote or hinder plant invasions in ways that alter basic ecosystem processes and feedback to other components of global change. Recent reviews suggest that rising atmospheric CO_2, N deposition, increased precipitation, and land use change usually promote plant invasions, although global warming and decreased precipitation may hinder plant invasions (Bradley et al. 2010; Sorte et al. 2013). Rising atmospheric CO_2, N deposition and increased precipitation directly enhance the availabilities of resources such as C, N, and water that plants require for their photosynthesis and growth. These components of global change often facilitate fast-growing invasive plants. For example, in a free-air CO_2 enrichment experiment in Wyoming (USA), elevated CO_2 increased photosynthesis by +87 % in the invasive forb *Linaria dalmatica* but only by +23 % in the native grass *Pascopyrum smithii* (Blumenthal et al. 2013) (Fig. 2.3). Furthermore, global warming has been documented to increase the growth of invasive plants in water-rich mesic ecosystems. However, warming-induced drought, or direct drought by decreased precipitation, potentially favours drought-tolerant native plants (Bradley et al. 2010; Sorte et al. 2013). Climate-induced ecosystem alterations in abiotic (e.g., temperature and moisture) and biotic (e.g., plant community composition) conditions are predicted to drastically mediate ecosystem C cycling (Bradley et al. 2010). Environmental change-induced increases in the prevalence of invasive plants might accelerate the changes in ecosystem C cycling. Furthermore, land use change by deforestation and land reclamation causes ecosystem disturbances that might harm native plants and increase resources, including space availability, for invasive plants (Bradley et al. 2010).

Although many experimental studies have been conducted to examine the dynamics of invasive plants under global change, the complexity of the interactions between invasive plants and global change limits our ability to draw firm conclusions on the feedbacks between plant invasions and ecosystem C cycling. In addi-

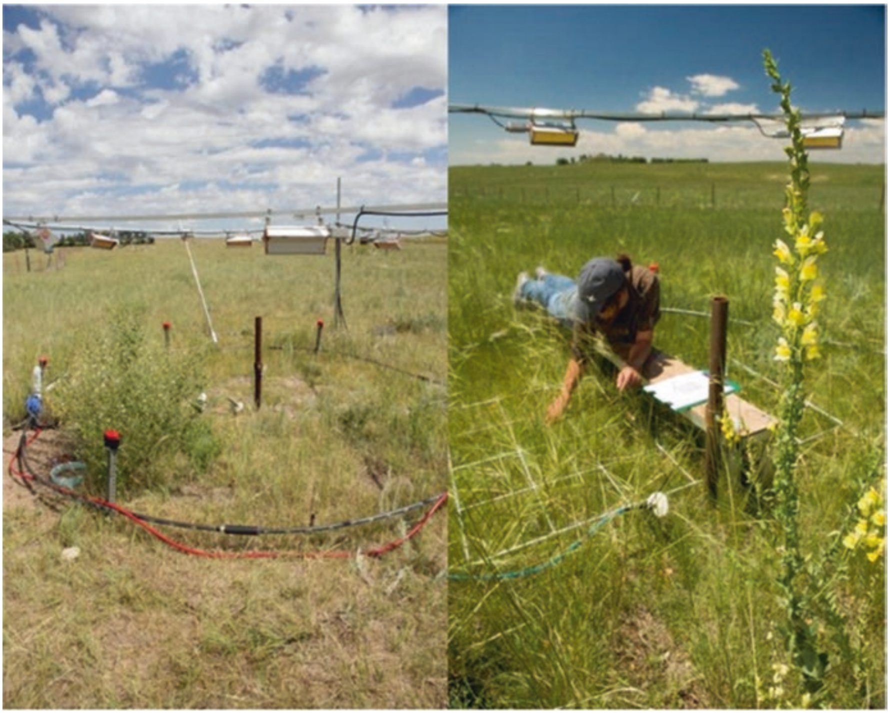


Fig. 2.3 Prairie Heating and CO_2 Enrichment (PHACE) experiment, which was partly designed to assess the effects of invasion of the forb *Linaria dalmatica* under climate change on a northern mixed-grass prairie located in Wyoming, USA. The experiment has imposed a factorial combination of two levels of CO_2 (ambient and elevated 600 ppmv), and two temperature regimes [ambient and elevated (1.5/3.0 °C warmer day/night)] (Photograph by Julie Kray)

tion, most studies to date have focused on the responses of invasive plants to a single component of global change, so little is known about the effects of multiple and interacting environmental variables on plant invasions and their feedbacks to ecosystem C cycling. Therefore, we highlight the urgent need for a multifactor experimental approach to understanding invasion-induced changes in ecosystem C processes in the context of multiple global environmental changes, and a combination of experimental and modeling studies to predict feedbacks between plant invasions and ecosystem C cycling.

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Chapter 3
Modification of Habitat Quality by Non-native Species

Jorge L. Gutiérrez

Abstract Non-native species can affect the quality of habitats available to other organisms and, in turn, the ecosystem services they provide or regulate. Although much research to date has focused on the impacts of non-native species on habitats, the links between habitat impacts and the provision or modulation of ecosystem services have remained elusive. This review illustrates two general kinds of non-native species impact on the abiotic conditions and resources available in a habitat: (1) assimilatory-dissimilatory impacts from the uptake and release of energy and materials and (2) physical ecosystem engineering impacts that arise from structural modification of environments caused by species presence and/or activities. Additionally, it distinguishes between physical ecosystem engineering impacts that result from the creation or modification of physical structures per se (e.g., effects on living space) and those that occur because of the interactions of physical structures and different forms of kinetic energy, such as heat or fluid flows (e.g., wind attenuation by trees). Examples are given to illustrate the co-occurrence of multiple impact pathways and their often compound impacts on single habitat attributes. Finally, the habitat-mediated impacts of non-native species on food and raw materials, climate, and tourism and recreation are discussed as examples of cascading impacts on provisioning, regulating, and cultural services, respectively.

Keywords Abiotic conditions • Ecosystem services • Ecological impact • Invasive species • Habitat • Ecosystem engineers • Resources • Physical structures

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3.1 Introduction

Non-native species can profoundly alter the habitat available to other organisms (Crooks 2002). In so doing, they can have significant knock-on effects on human well-being because a variety of the benefits that humans derive from ecosystems—or ecosystem services—are contributed or modulated by organisms. Given the dependence of many ecosystem services on the abundance and activity rates of organisms, habitat is often considered as part of the supporting functions or structures (Farber et al. 2006), or simply supporting services on which other kinds of ecosystem services depend. Although impacts on habitats have been largely documented in the literature, the consequences of these effects in the provision or modulation of ecosystem services are nevertheless less appreciated.

This chapter reviews the distinct kinds of non-native species impacts on the quality of habitats available to other organisms. It focuses on the habitat-mediated impacts of these species on food and raw materials, climate, and tourism and recreation as examples of cascading impacts on provisioning, regulating, and cultural services, respectively. Habitat is defined here as the physical place where organisms live (Farber et al. 2006), which includes its physical structure as well as the consumable resources and abiotic conditions that produce occupancy (Hall et al. 1997). In this same vein, habitat quality is defined as the property of the environment to provide the physical structure, consumable resources, and abiotic conditions appropriate for occupancy by a focal species (Hall et al. 1997).

3.2 Impacts on Habitat Quality

Most of the mechanisms that underlie the impact of non-native species on habitats can be broadly classified as assimilation-dissimilation or physical ecosystem engineering impacts (sensu Jones and Gutiérrez 2007). These effects encompass impacts on the physical structures, consumable resources, and abiotic conditions that define habitat quality for other species (Gutiérrez et al. 2014).

Assimilation-dissimilation involves the uptake (assimilation) of energy and materials (e.g., light, water, nutrients, other minerals, O_2, CO_2, trace gases, organic compounds) and their release (dissimilation) in the form of dead tissues and waste products (e.g., carbon and nutrients in litter; woody debris; faeces, urine, and carcasses; water, O_2, CO_2, trace gases, H^+, and other organic and inorganic chemicals). Assimilatory-dissimilatory transfers encompass all kinds of autotrophic, mixotrophic, and heterotrophic interactions (e.g., plant uptake and litter production; herbivory, predation, detritivory, microbial uptake and release).

Physical ecosystem engineering, in contrast, arises from the structural modification of the environment caused by the presence or activities of organisms (Jones et al. 1994). Examples include wind attenuation by trees, animal burrowing, dam-building by beavers, and soil compaction by large mammals. Such structure-mediated

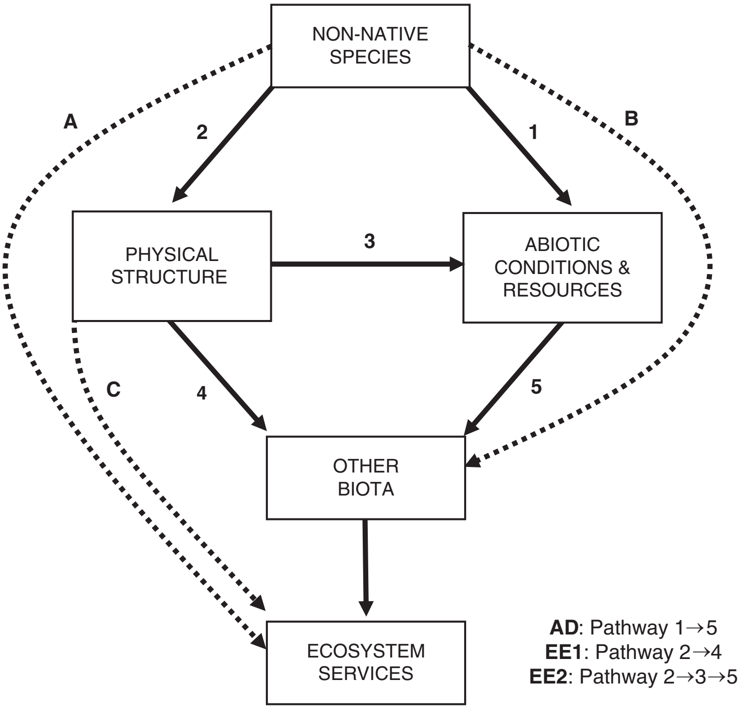

Fig. 3.1 Non-native species impacts on habitat quality and consequences for other ecosystem services. The *solid arrows* represent pathways of impact that involve changes in habitat quality, including assimilatory-dissimilatory (AD) impacts that result from the uptake and release of energy and materials by non-native species, and physical ecosystem engineering (EE) impacts that arise from structural modification of the environment because of the presence or activities of the non-native species. Distinction is made here between engineering impacts that result from the creation or modification of physical structures per se (EE1) and those that occur because of the interactions of physical structures and different forms of kinetic energy, such as heat or fluid flows (EE2). The *dotted arrows* represent non-native species impacts on ecosystem services that occur irrespective of habitat changes, namely, direct assimilatory-dissimilatory impacts (*pathway A*), consumption of organisms involved in the provision or modulation of services (*pathway B*), and direct effects of engineered structures (*pathway C*)

effects are often associated with assimilatory and dissimilatory transfers to varying degrees (e.g., soil reworking by feral pigs when foraging on roots). Nonetheless, the effects of structure on the abiotic conditions and consumable resources available to other organisms cannot be predicted from the nature and magnitude of these transfers alone. Considering the aforementioned example, the effects of feral pigs on soil topography will depend on foraging rates but also on baseline soil properties, vegetation cover, rainfall, and evaporation (Jones and Gutiérrez 2007).

Assimilatory-dissimilatory (AD) and physical ecosystem engineering (EE) pathways of non-native species impact on habitat quality are represented in Fig. 3.1. Assimilation-dissimilation affects habitat quality via changes in resource availability and abiotic conditions that result from the consumption or provision of energy and materials in the form of living or dead tissues and metabolic end-products (AD: pathway 1 → 5 in Fig. 3.1). Ecosystem engineering involves changes on the physical structure of the habitat. Such structural changes may lead to altered habitat quality per se (e.g., availability of physical living space or nesting sites) (EE1: pathway 2 → 4 in Fig. 3.1), or interact with distinct forms of kinetic energy thus altering the abiotic conditions and the availability of consumable resources via dissipation, reflection, and conversion along with material redistribution (e.g., tree effects on understory temperature, flow attenuation, and organic matter deposition in macrophyte beds) (EE2: pathway 2 → 3 → 5 in Fig. 3.1). Impacts on habitat quality via these pathways are outlined next and exemplified in detail in Table 3.1.

3.2.1 Assimilatory-Dissimilatory Impacts on Abiotic Conditions and Consumable Resources

Assimilatory-dissimilatory effects of non-native species on the abiotic conditions and consumable resources available to other organisms can result from the consumption of materials and energy (e.g., food, water, nutrients, light) or their supply in the form of living (e.g., leaves, fruit, animal tissues) or dead matter (e.g., litter, carrion) and metabolic end-products (e.g., faeces, urine, allelochemicals). Effects resulting from material and energy consumption include reduced light levels in the understory of non-native trees (Reinhart et al. 2006), decreased phytoplankton biomass in rivers and lakes as the result of filter feeding by non-native invertebrates (Sousa et al. 2009), and macrophyte biomass decreased by consumption by non-native grazers (e.g., the golden apple snail, *Pomacea canaliculata,* in southeastern Asia wetlands and rice fields; Horgan et al. 2014).

Examples involving the supply of energy and materials include altered organic matter quantity and quality in soils resulting from inputs of non-native plant litter, increased food supply to frugivores caused by the establishment of non-native fruiting plants [e.g., glossy privet, *Ligustrum lucidum,* in the subtropical forests of northwestern Argentina], and toxic water column ammonia levels caused by invasive bivalve die-offs (e.g., *Corbicula fluminea* in southeastern US rivers).

3.2.2 Physical Ecosystem Engineering Impacts on Habitat Structure

A pervasive example of non-native species impact on habitat quality that results from the creation or modification of physical structures per se is the provision of living space to other organisms in aquatic environments, either in the form of hard substrate for attachment or structural refugia against consumers (Jones et al. 2010). Examples include aquatic macrophytes (e.g., the common reed *Phragmites*

Table 3.1 Non-native species impacts on habitat quality and their underlying mechanisms. See Fig. 3.1 for more details and Figs. 3.2 and 3.3 for illustrations

Species (origin)	Case study	Habitat impacts	Mechanism (Pathways)	References
Blue-leafed wattle *Acacia saligna* (Western Australia)	South African fynbos	Soil N and organic matter (+)	Large inputs N-rich litter (AD)	(1)
		Light irradiance and soil temperature (−)	Shading and altered heat transfer (AD-EE2)	(1)
		Water yield in catchments (−)	Root uptake (AD)	(2)
Amur honeysuckle *Lonicera maackii* (China and Japan)	Midwestern US forests	Allelopathy (Q)	Release of allelochemicals (AD)	(3)
		Light irradiance in the forest floor (−)	Shading (AD-EE2)	(4)
		Food supply to some frugivorous birds (+)	Fruit production (AD)	(5)
		Bird nesting sites (+, −, Q)	Altered habitat architecture (EE1)	(6)
Iceplant *Carpobrotus edulis* (South Africa)	Californian coastal scrub	Water availability (−)	Root uptake (AD)	(7)
		Food availability to some mammals (+)	Fruit production (AD)	(8)
		Soil carbon content (+) and pH (−)	Decomposition (AD)	(9)
Smooth cordgrass *Spartina alterniflora* (Atlantic coast of the Americas)	Southeastern China salt marshes	Soil accretion rates (+)	Sedimentation (EE2), and dead-root accumulation (EE1)	(10)
		Food quality for grazing crabs (+)	Biomass production (AD)	(11)
		Space available to ground foraging birds (−)	Preemption by dense canopies (EE1).	(12)
Red seaweed *Gracilaria vermiculophylla* (Northwest Pacific)	Southeastern US estuary mudflats	Food supply to grazers (+)	Biomass production (AD)	(13)
		Food supply to detritivores (+)	Addition of highly decomposable litter (AD)	(13)
		Interstitial space for mobile invertebrates (+)	Formation of dense algal mats (EE1)	(14)
Earthworms *Lumbricus terrestris* and several other species (Europe and Asia)	Northeastern US forests	Surface litter cover (−)	Litter consumption/burial (AD/EE1)	(15)
		Soil porosity (+) and nutrient leaching (+)	Particle aggregation and burrowing (EE1, EE2)	(15)
		Microhabitats to soil arthropods (Q)	Construction of burrows and middens (EE1)	(16)
		Food supply to some consumers (+)	Biomass production (AD)	(16)

(continued)

Table 3.1 (continued)

Species (origin)	Case study	Habitat impacts	Mechanism (Pathways)	References
Gypsy moth *Lymantria dispar* (Eurasia and Northern Africa)	Northeastern US mixed-oak forests	Leaf-litter inputs to soils (−)	Tree defoliation by caterpillars (AD)	(17)
		Inputs of labile C and N to soils (+)	Production of feces or frass (AD)	(17)
		Food base to some birds and mammals (+)	Biomass production (AD)	(18)
		Light penetration to the forest floor (+)	Reduced tree canopy cover (EE2)	(17)
		Runoff and soil erosion (+)	Reduced tree transpiration, increased throughfall (AD-EE2)	(17)
Zebra mussel *Dreissena polymorpha* (Eastern Europe and Central Asia)	Hudson River Estuary, NY, USA	Phytoplankton densities (−)	Filter feeding (AD)	(19)
		Light penetration into water column (+)	Removal of suspended particles (EE2)	(19)
		Interstitial space for mobile invertebrates (+)	Mussel aggregation into dense matrices (EE1)	(19)
		Hard substrate for organismal attachment (+, Q)	Shell production (EE1)	(19)
		Benthic organic matter (+)	Biodeposition (AD)	(19)
Reef-forming polychaete *Ficopomatus enigmaticus* (Australia)	Mar Chiquita Coastal Lagoon, Argentina	Phytoplankton concentrations (−)	Filter feeding (AD)	(20)
		Benthic organic matter (+)	Biodeposition (AD)	(21)
		Hard substrate for organismal attachment (+, Q)	Production of calcareous tubes by worms (EE1)	(22)
		Interstitial space (+, Q)	Reef formation by tube-building worms (EE1)	(23)
		Emergent seabird resting sites (+)	Reef formation by tube-building worms (EE1)	(24)
		Sedimentation (+)	Flow attenuation by reefs (EE2)	(25)
Common carp *Cyprinus carpio* (Eurasia)	Central Mexico shallow ponds	Macrophyte abundance (−)	Grazing (AD)	(26)
		Invertebrate prey (−)	Predation (AD)	(26)
		Sediment resuspension and turbidity (+)	Macrophyte uprooting and sediment reworking (EE2)	(27)

Beaver *Castor canadensis* (North America)	Tierra del Fuego Archipelago, Chile	Riparian forest cover (−)	Foraging and flooding from dam building (AD-EE2)	(28)
		Flow velocities (−)	Dam building (EE2)	(29)
		Sedimentation and benthic organic matter (+, −)	Flow attenuation by dams (EE2)	(29)
Feral pigs *Sus scrofa* (Eurasia)	Hawaii, USA	Food supply to primary consumers (+, −, Q)	Foraging, trampling, uprooting, and tusking (AD-EE1)	(30)
		Water pools in soils and tree trunks (+)	Wallowing and foraging on the pulp of tree ferns (EE2)	(30)
		Soil erosion (+)	Soil reworking and reduced plant cover (EE2)	(30)

Impacts are characterized as quantitative, including increases (+) or decreases (−) in resources or abiotic variables; or as qualitative (Q) when resulting from the generation of resources or abiotic conditions that are novel to some recipient organisms. Mechanisms are classified as assimilatory-dissimilatory (AD), physical ecosystem engineering (EE), and compound ones (AD-EE). Distinction is made between engineering impacts on habitat quality that results from the creation or modification of physical structures per se (EE1), and those that occur because of the interplay between such physical structures and different forms of kinetic energy (EE2)

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Other cases include architectural effects of non-native plants on the amount and suitability of nest or perching sites available to birds, and physical restriction of movement in ground-foraging birds by dense, invasive plant canopies (Gan et al. 2009).

3.2.3 Physical Ecosystem Engineering Impacts on Abiotic Conditions and Consumable Resources

The diverse physical effects of non-native plant canopies on abiotic conditions and the fluxes of energy and materials in their understory are chief examples of changes in habitat quality resulting from the interaction between the structures made by non-native species and kinetic energy. The interaction includes light absorption and reflection by canopies which, together with light assimilation (i.e., photosynthesis), can substantially alter irradiance levels in the understory (Reinhart et al. 2006). Non-native plant canopies also dissipate/reflect/convert the energy of fluid flows (wind, water), increasing the deposition of particulate and dissolved matter. The latter is well illustrated by the effects of non-native tree plantations on the deposition of wind-borne sediments (e.g., sand deposition in *Eucalyptus camaldulensis* plantations in Israel; Karschon 1960) as well as pollutants and nutrients (e.g., sulfur and nitrogen deposition in Sitka spruce, *Picea sitchensis*, plantations in northern England; Fowler et al. 1989). Analogous effects occur because of water flow attenuation by macrophytes in aquatic ecosystems (e.g., enhanced sedimentation in *Phragmites australis* marshes in North America; Kiviat 2013).

In addition, the structures built or physically modified by non-native animals can also impact habitat quality by interacting with distinct forms of kinetic energy. Selected examples include non-native earthworm burrows, primarily *Lumbricus terrestris* and *L. rubellus*, that accelerate water infiltration with concomitant increases in nutrient leaching from soils in northeastern US forests (Bohlen et al. 2004); dams built by the introduced beaver, *Castor canadensis,* on Tierra del Fuego Island that attenuate stream flow leading to upstream pond formation, concomitant deposition of suspended sediments and organic matter, and decreased downstream sedimentation (Anderson et al. 2009); and dense networks of burrows made by the non-native isopod *Sphaeroma quoyanum* which weaken salt marsh banks, facilitating their erosion and conversion into unvegetated tidal flats in San Diego Bay and San Francisco Bay, USA (Talley and Crooks 2007).

3.2.4 *Compound Impacts on Single Habitat Attributes*

As the impacts of plant canopies on understory light irradiance illustrate (see Sect. 3.2.3), non-native species can affect a single habitat attribute via a combination of distinct, concurrent mechanisms, such as photosynthesis and light absorption/reflection. The elimination of riparian forests by beavers in the Tierra del Fuego archipelago also well exemplifies this point, as it occurs because of beaver foraging on seedlings and flooding of the riparian zone as a consequence of dam building (Anderson et al. 2009). Another example in this regard is the development of hypoxia in beds of the floating-leaved macrophyte *Trapa natans* in the shallows of the Hudson River estuary (New York, USA). This species is alleged to deplete oxygen from the water column at least via three mechanisms (Caraco et al. 2006). First, it photosynthesizes in the overlying atmosphere but has substantial amounts of submersed respiratory tissues, which implies that it vents oxygen to the atmosphere to produce organic carbon that, in a significant part, is respired underwater. Second, the dense and thick mats of floating leaves in this species inhibit light penetration and, thus, primary production and oxygen release by other submersed plants. Third, extensive coverage by this species limits the development of turbulence at the air–water interface, thus reducing gas exchange and atmospheric oxygen inputs.

Clearly, the co-occurring mechanisms underlying the compound impacts on a given habitat attribute may not equally be influenced by variations in environmental conditions or the phenological or population status of the species. For instance, early leaf senescence in *T. natans* might have little impact on light penetration and turbulence at the air–water interface but have a significant impact on photosynthesis and respiration. Therefore, recognising these component mechanisms is important to address how their relative contributions drive spatial and temporal variations in overall, compound effects (Gutiérrez et al. 2014).

3.2.5 *Concurrent Impacts on Multiple Habitat Attributes*

As becomes evident from the examples in Table 3.1, non-native species usually have simultaneous impacts on distinct habitat attributes. They may combine assimilation-dissimilation, physical ecosystem engineering, and compound influences (Table 3.1). Concurrent impacts on habitat attributes can be causally linked (e.g., tree impacts on light regimes and understory temperatures) or bear no apparent relationship to each other (e.g., tree impacts on soil moisture and the availability of nesting sites for birds).

Certainly, not all the habitat attributes concurrently affected by a non-native species are necessarily relevant to a focal species. Yet, apparently insignificant habitat attributes can often mediate impacts on a focal species via complex causal connections. For example, decreases in phytoplankton biomass caused by filter feeding by non-native zebra mussels may be judged beforehand as inconsequential to fishes that feed on benthic and epiphytic invertebrates. Nonetheless, phytoplankton consumption by zebra mussels increases water clarity and the depth of the photic zone, thus increasing the areal cover and biomass of light-limited rooted macrophytes, as well as the abundance of invertebrates that feed on or live amongst these plants and are prey for the fishes in question (Strayer et al. 2004). The foregoing sequence of changes in habitat attributes likely explains increases in invertebrate-feeding littoral fish after zebra mussel invasion (Strayer et al. 2004) and also serves to illustrate that a focus on a single habitat attribute or the most obvious ones affected by non-native species may fall short to characterise changes in habitat quality to focal species, as well as to predict their numerical responses.

3.3 Habitat-Mediated Impacts on Other Ecosystem Services

Non-native species can affect habitat attributes with consequences on the abundance or activity rates of organisms involved in the provision or modulation of other ecosystem services (Figs. 3.2 and 3.3). Such habitat-mediated effects are a subset of the impacts that non-native species can have on ecosystem services. Clearly, many of the impacts of non-native species on ecosystem services occur irrespective of their

Fig. 3.2 Iceplant, *Carpobrotus edulis*, colonizing a coastal dune field in San Eduardo del Mar, Argentina (Photograph by Jorge Gutiérrez)

Fig. 3.3 Reefs built by the non-native polychaete *Ficopomatus enigmaticus* in Mar Chiquita coastal lagoon, Argentina (Photograph by Martín Bruschetti)

effects on the habitat available to other organisms (pathways A–C in Fig 3.2) (see examples in Catford 2017; Fried et al. 2017; Gaertner et al. 2017; Nie et al. 2017). Here, habitat-mediated impacts of non-native species on food and raw materials, climate regulation, and tourism and recreation are examples of cascading impacts on provisioning, regulating, and cultural services, respectively.

3.3.1 Food and Raw Materials

Non-native species affect the quality of habitats of a variety of species that are sources of food and raw materials to humans. In fact, the deliberate introduction of non-native species to enhance habitat quality for such species has been widespread. For instance, there is a long tradition of intentional non-native plant introductions in rangelands to increase forage yield and quality and, ultimately, livestock production. However, there also are several accidentally introduced plants that are unpalatable or toxic to cattle and thus have opposite effects on the quality of rangelands as livestock habitat. Accidentally introduced non-native plants (weeds) can also reduce crop production (Fried et al. 2017) by altering the light environment, consuming soil nutrients, or releasing allelochemicals (Rajcan and Swanton 2001).

The effects of non-native species on habitat attributes also have implications for wild sources of food to humans. For example, freshwater aquatic macrophytes such as the water hyacinth, *Eichornia crassipes,* affect fish habitat in their nonnative ranges by concurrently altering its physical structure (e.g., shelter, space preemption), resources (e.g., prey availability), and abiotic conditions (e.g., oxygen levels). These habitat changes can increase or decrease stocks of commercially important fishes, depending on the requirements of the species in question (Villamagna and Murphy 2010 for a review). Analogous habitat-mediated impacts on economically important fish or shellfish are also documented for marine ecosystems or in response to other habitat-forming non-native species, such as non-native macroalgae or bed-forming bivalves (Jivoff and Able 2003; Strayer et al. 2004).

3.3.2 Climate Regulation

Some non-native species often substantially affect soil physical structure (e.g., aggregate size), resources (e.g., organic matter quantity and quality, N, P), or abiotic conditions (e.g., moisture, redox potential) with consequences for the abundance and activity rates of microorganisms involved in the decomposition of organic matter and the emission of greenhouse gases (Nie et al. 2017). These habitat modifications contributed to increased CO_2 emissions as agriculture and non-native crops expanded across the globe (Lal 2004). However, the net contribution of soil modification by crops to CO_2 emissions is generally hard to separate from the effects of crop management (e.g., tillage, fertilizer, and pesticide use).

The impacts of soil habitat modification by non-native species on microbial processes and greenhouse gas emissions are particularly well documented in wetlands, whose primarily anaerobic soils are a favourable habitat for microbes that decompose organic matter into methane. Non-native plants in wetlands can either increase (Mozdzer and Megonigal 2013) or decrease (Grand and Gaidos 2010) methane emissions. Such changes can be attributed to altered root biomass, productivity, and oxygen release rates and, thus, altered availability of organic carbon or electron acceptors (e.g., oxygen and ferric iron), which jointly regulate the total amount of anaerobic microbial respiration and methane production in soils (Sutton-Grier and Megonigal 2011). Given that wetlands contribute about a third of global methane emissions, widespread non-native plant establishment in wetlands might be significant vis-à-vis climate impacts.

A striking impact on the habitat of methane-producing microbes is that of the beaver, which creates wetlands via dam building. Methane emissions associated with non-native beaver ponds in the Tierra del Fuego archipelago are estimated to amount to about 2.7 Gg $year^{-1}$ (Whitfield et al. 2015). Other impacts of non-native animals on greenhouse gas emissions from soils or sediments include enhanced CO_2 and methane emissions from tidal flats after oyster establishment, which likely results from increases in sedimentary organic carbon from biodeposition and enhanced sedimentation amongst oyster shells (Green et al. 2012); or earthworm-induced increases in CO_2 and N_2O emissions, which partially result from local enrichment of mineral N, available C, and moisture in casts and burrow walls (Lubbers et al. 2013). Although the contributions of these animals are apparently minor at the global scale, they might represent important regional sources of gas emissions.

3.3.3 Tourism and Recreation

Non-native species often cause habitat-mediated impacts on the abundance of charismatic species that are an attraction for ecotourism, such as the Atlantic puffin, *Fratercula arctica*, in Scotland and the critically endangered Montserrat oriole, *Icterus oberi*, on Montserrat Island. Breeding success and size in colonies of the Atlantic puffin have been negatively affected by the spread of non-native tree mallows, *Lavatera arborea*, (Fischer and van der Wal 2007). Similarly, nesting sites for Montserrat orioles have been lost as a consequence of livestock foraging on their primary nesting plants (Peh et al. 2015). Some non-native macrophytes also have habitat-mediated impacts on fish species that are targets of recreational fishing (Slipke et al. 1998).

3.4 Conclusions

This review outlines and exemplifies the general mechanisms of non-native species impacts on habitat quality and the impacts of such habitat changes on other ecosystem services. The habitat-mediated impacts of non-native species on ecosystem services seem to be underreported in the literature relative to their overall impacts on habitat quality. This lack is likely because much of the research on the impacts of non-native species on habitats has been motivated by an interest in the conservation of species and communities, and their habitats, in spite of the services that the species in question may provide. A greater understanding of the links between habitats, species, and ecosystem services, as presented in this review with regard to habitat modification by non-native species, can contribute to a full picture of the costs and benefits of anthropogenic habitat transformation.

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Chapter 4
Alteration of Nitrogen Cycling as a Result of Invasion

Pilar Castro-Díez and Álvaro Alonso

Abstract The invasion of ecosystems by non-native species may alter the nitrogen (N) cycle through different nonexclusive mechanisms. Dramatic alterations occur in an ecosystem when the invasive species possesses a new strategy to acquire this nutrient, such as N_2 fixation ability. Gradual alterations are caused by changes in the utilisation of N with respect to dominant natives, such as changes in N allocation patterns, which affect the chemical composition of tissues and therefore the decomposition and mineralisation processes. Changes in the disturbance regime mediated by plant invasion, and alteration of the trophic structure caused by the invasion of non-native animals, may also have profound effects on the N cycle. Published synthesis studies suggest that, altogether, plant invasions tend to increase N pools and to accelerate N fluxes of the invaded ecosystems. However, particular impacts are highly dependent on the context and therefore difficult to predict. A critical review of these syntheses shows that the available literature on invaders' impacts is highly biased in the selection of species, impact metrics, and ecosystem types. These biases suggest that, in spite of great advances in understanding the impacts of invaders on the N cycle, more information is needed on the impacts of many invaders so far ignored, on how invaders change the net ecosystem gains and losses of N, and on the role of the context.

Keywords Decomposition • Disturbance • Mineralisation • N allocation • N cycle • N fixation • N flux • N pool

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4.1 Introduction

Nitrogen (N) is the fourth most abundant element in living tissues, only behind oxygen, carbon and hydrogen. It forms part of proteins, DNA, chlorophyll, etc. Although N is very abundant on Earth, particularly in the atmosphere where it appears as N_2, it is not accessible for most plants in this form. This N_2 remains inaccessible to plants until specific microorganisms break down the bonds between the N molecules, thereby freeing N atoms that can then bond with hydrogen or oxygen to form accessible inorganic compounds (mainly ammonia NH_4^+ or nitrate NO_3^-). This N fixation is an important biological process and is primarily mediated by living organisms (microbes), although some N fixation can also occur in the atmosphere using the energy of lightning discharges without the involvement of living organisms. Once N has been converted to accessible inorganic forms, it enters the biological pathways of the N cycle (Fig. 4.1), where it cycles between organic and inorganic compartments. A relevant part of N gets locked up in the soil organic matter, which must be decomposed by microorganisms before being available for most plants. Given the bottlenecks of N fixation and organic matter mineralization, N becomes in one of the major limiting factors of primary production controlling the functioning and structure of many ecosystems.

Similar to other nutrient cycles, the N cycle is considered as a supporting ecosystem service that is necessary for the maintenance of other services. For instance, the production of plant-derived goods (food, wood, fibre, etc.) depends on primary production, which in turn depends on N availability. Water quality is largely mediated by plants growing in floodplains, estuaries, or marshlands and their influence on nutrient cycling, while climate regulation is linked to the N cycle both directly, because of the greenhouse power of some N oxides that are emitted in the combustion of organic matter, and indirectly, by controlling the growth of plants and phytoplankton, which are the major sinks of CO_2.

We are deeply aware of the strong alterations that certain human activities have caused to the N cycle and the associated ecosystem services (Vitousek et al. 1997; Galloway et al. 2004; Shibata et al. 2015). Humans have dramatically increased the annual N_2 fixation by the industrial production of N fertilizers. By extending the amount of land devoted to the cultivation of N_2-fixing plants (mainly those of the Fabaceae family), humans have additionally contributed to a substantial increase of biotic N_2 fixation. The burning of forests, grasslands, or wood liberates N from long-term biological storage pools, and the burning of fossil fuels does the same with long-term geological storage. In both cases, the N is released in the form of N oxides (NO and N_2O) into the atmosphere, where the oxides may contribute to greenhouse warming (NO), stratospheric ozone depletion (NO), and acid rain (N_2O). Human activities have also increased nutrient inputs to aquatic ecosystems: 2.2 fold for nitrate and 4 fold for ammonia (Goudie 2006). Overall, these alterations contribute to increasing the stocks of biologically available N and to speeding up the N transfers among different storage forms (Vitousek et al. 1997; Galloway et al. 2004; Shibata et al. 2015).

The alteration of the N cycle by non-native species has been less well studied. This topic started to receive the attention of scientists and land managers at the end of the 1980s. Given that some invasive plants differ from the natives in N uptake strategy and/or N utilisation, they have the potential to alter the N cycle. In addition, some aquatic invasive animals may alter the N cycle increasing the concentration of growth-limiting nutrients and accelerating transformations. This chapter reviews the mechanisms by which invasions by non-native species may alter the N cycle in terrestrial and in aquatic ecosystems, and explores whether there are general trends on the impact of invaders on the N cycle.

4.2 Mechanisms of N Cycle Alteration by Invasions

Non-native invasive species may alter the N cycle, either by changing the size of N storage in different compartments of the ecosystem (diamonds in Fig. 4.1) or by changing the rate at which N is transferred (arrows in Fig. 4.1). Based on Vitousek

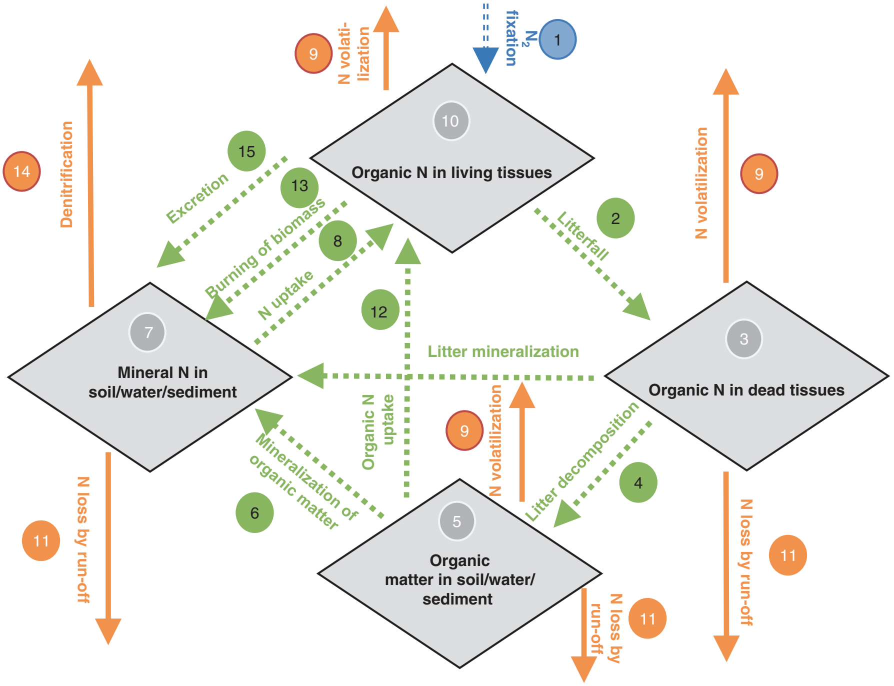

Fig. 4.1 Schematic representation of the nitrogen (N) cycle. *Diamonds* indicate N pools in different chemical forms and ecosystem compartments. *Dashed arrows* indicate N fluxes between different pools, *solid arrows* represent ecosystem N losses, and the *double-dashed arrow* indicates ecosystem N inputs. *Numbers* identifying each pool or flux are mentioned throughout the text and in Tables 4.1 and 4.2

(1990), we suggest four types of nonexclusive ways by which invaders can change ecosystems: by differing from natives in the strategy of (1) N acquisition or (2) N utilisation; (3) by altering the disturbance frequency or intensity; and (4) by altering the trophic structure of the community. This section reviews each of these mechanisms, using examples to illustrate them.

4.2.1 Changes in the Strategy of N Acquisition

Ecosystems can change dramatically when newly introduced non-native species have access to N sources that are not available to native species within that ecosystem. In contrast, gradual alterations occur when non-natives differ from natives in the magnitude of any functional trait controlling the rate of N transfer across ecosystem compartments (Chapin et al. 1996). This section considers dramatic changes resulting from new strategies of N acquisition; gradual alterations are addressed in the next section.

The best known mechanism of dramatic N cycle alteration by invasive species is the introduction of plants with mutualistic N_2-fixing microorganisms in ecosystems lacking such symbioses. The additional N input is first stored in the plant biomass, but it rapidly cycles within the ecosystem, increasing the size of one or more N pools. Higher N availability in the soil may also stimulate metabolic reactions of decomposers, along with their population growth, leading to a faster processing of organic matter. This alteration was first illustrated by the actinorhizal N_2-fixing shrub, *Moreya faya*, invading young N-poor volcanic soils in Hawaiian islands in the late 1800s. Given the lack of N_2-fixers in this early-succession rainforest, the invasion of *Moreya* quadrupled the input of fixed N_2 in the ecosystem and enhanced N mineralisation, making this extra N available to plants (Vitousek and Walker 1989). This seminal study on the scientific community launched the search for other case studies, where N_2-fixing non-native plants also invaded N-poor systems, with similar impacts (Table 4.1).

Another potential new strategy of N acquisition might be the ability of non-native plants to uptake N in organic form in communities with no or little ability to do so, which would lead to a shortcut in the N cycle (see path 12 in Fig. 4.1). This mechanism was suggested to explain the changes on soil properties caused by invasive *Hieracium pilosella* in heavily grazed tussock grasslands in New Zealand. Soils beneath this invader showed increased organic N and C accumulation, as well as C mineralisation. However N mineralisation was decreased in the invaded soils. The suggested explanation for this pattern was that *Hieracium*—thanks to the high levels of polyphenols in its leaves—inhibits N mineralisation and leads to the accumulation of organic N in the soil. At the same time, *Hieracium* would be able to take up organic N, benefiting from its own soil transformation (Saggar et al. 1999). However, no other evidence of this mechanism has been found in the literature, and further research is needed to check the extent to which this mechanism impacts the N cycle.

Table 4.1 Summary of mechanism of N cycle alteration by non-native species and examples reported in the literature

Mechanisms	Examples	References	Reported effect[a]	Affected pool/flux
Invasive plants support symbiotic N_2 fixers	Invasion of young volcanic soils of Hawaii by *Moreya faya*	Vitousek and Walker (1989)	N fixation + N mineralisation + soil mineral N +	(1/6/7)
	Invasion of South African fynbos by *Lupinus luteus* and *Acacia saligna*	Yelenik et al. (2007)	Soil mineral N +	(7)
	Invasion of Portuguese coastal dunes by *Acacia longifolia*	Marchante et al. (2008)	Soil N +	(5/7)
Changes in dominant life/growth form	Invasion of perennial-dominated short-grass steppe of Colorado by the annual *Kochia scoparia*	Vinton and Burke (1995)	N mineralisation +	(6)
	Invasion of perennial-dominated Californian grasslands by non-native annuals	Parker and Schimel (2010)	Soil ammonium + nitrification +	(7/6)
	Invasion of New Zealand broadleaf forests by the perennial herb *Tradescantia fluminensis*	Standish et al. (2004)	Litter decomposition + soil mineral N +	(4/7)
	Invasion of New Zealand tussock grasslands by conifers	Harding (2001)	Plant N uptake +, plant biomass +	(8/10)
Changes in tissue quality	Invasion of Californian serpentine annual grasslands by the annual *Aegilops triuncialis*	Drenovsky and Batten (2007)	Plant biomass + litter decomposition −	(10/4)
	Invasion of a mixed forest in Wisconsin by the shrub *Frangula alnus*	Stokdyk and Herrman (2014)	N mineralisation +, soil mineral N +	(6/7)
	Invasion of NW Spain forests by *Eucalyptus globulus*	Castro-Díez et al. (2012)	Litter decomposition − Nitrification −	(4/6)

(continued)

Table 4.1 (continued)

Mechanisms	Examples	References	Reported effect[a]	Affected pool/flux
Changes in disturbance regime	Fire increase by African grasses invasion in Hawaii *Metrosideros* forests	Ley and D'Antonio (1998)	N_2 fixation −	(1)
	Soil disturbance by *Sus scrofa* invasion in the Monte Desert biome (Argentina)	Cuevas et al. (2012)	N mineralisation +, soil mineral N +	(6/7)
Altered trophic structure	Invasion of NE-US forests by earthworms of the genus *Amynthas*	Burtelow et al. (1998)	Soil organic matter − Mineralisation + denitrification +	(5/6/14)
	Invasion of the American red swamp crayfish (*Procambarus clarkii*) in floodplain wetlands	Angeler et al. (2001)	N in water column +	(5/6)
	Invasion of lake Erie by the freshwater mussels *Dreissena polymorpha* and *D. bugensis*	Conroy et al. (2005)	N excretion +	(15)

The last column indicates the impacted N pool or flux according to Fig. 4.1

[a] + and − mean that the invasion increases and decreases the pool or flux, respectively

4.2.2 Changes from a Different Utilisation of N

Plant functional properties, such as growth rate, plant/leaf longevity, or growth form, largely determine the properties of the N cycle. Slow-growth plant species tend to produce long-lasting tissues by prioritizing investment in defence and support over growth; these tissues decompose at a slow rate, leading to a slow N cycling and to a high proportion of N locked up in organic forms. By contrast, fast-growth plant species tend to produce N-rich tissues by prioritizing production over defence and support. These tissues rapidly decompose and mineralise, leading to a fast N cycling. Similarly, annual plants invest their entire annual N budget in growth and reproduction, whereas perennial plants may divert part of their budget to storage, slowing down the N cycle. Also, large growth forms, such as trees, must invest more resources in long-life support tissues than smaller growth forms, such as herbaceous plants. Accordingly, when a non-native plant differs in growth rate, longevity, or growth form from those prevailing in the native community, the plant tissue quality may change and the N cycle may be altered. As already explained, this type of alteration may be considered as "gradual," so that the magnitude of these impacts would increase with the functional difference between the invader and the natives in the recipient ecosystem.

The addition of fertiliser in short-grass perennial-dominated steppe sites in Colorado promoted the invasion by the annual non-native grass *Kochia scoparia*. The litter properties of the annual invader increased the N cycling in soils of invaded sites (Vinton and Burke 1995). Similarly, in a podocarp-broadleaf forest in New Zealand, litter decomposition rate and N availability were found to be larger in soils beneath the invading perennial herb *Tradescantia fluminensis* than beneath uninvaded forests, where the vegetation is dominated by trees and shrubs (Standish et al. 2004). In New Zealand tussock grasslands, invasive conifer trees, which are much taller and have much deeper roots than native grasses, take up and hold more nutrients than the native community, presumably through increased mineralisation of the soil organic matter or through nutrient transfer from deeper soil horizons (Harding 2001).

Even if there is no change of the dominant life form or growth form after invasion, the tissue quality and quantity of the new dominant plant may be different from most natives in the recipient ecosystem, altering the N cycle. For instance, the non-native annual grass *Aegilops triuncialis*, which invades Californian serpentine annual grasslands, increases aboveground biomass twofold and produces a litter with higher lignin:N and C:N ratios, which decomposes less rapidly than litter from non-invaded plots (Drenovsky and Batten 2007). Litter produced by the non-native tree *Eucalyptus globulus* decomposes at a lower rate and drastically declined nitrification as compared with coexisting native trees in northwest Spain, probably because of its low N and high content of soluble polyphenols (Castro-Díez et al. 2012). Many species of the *Pinus* genus, naturalised mainly in the Southern Hemisphere, tend to decline the quality of the litter, which is often poorer in N and richer in lignin and secondary compounds than that of coexisting native trees. Consequently, pine introduction has been often found to deplete nutrients from upper mineral soil layers and to accumulate them in the overlying organic layer, and also to decrease N mineralisation as a result of its negative effects on soil bacteria (Simberloff et al. 2010; Scholes and Nowicki 1998). Further examples of changes to the N cycle by changes in the utilisation of N can be found in Table 4.1.

4.2.3 Alterations Mediated by Disturbances

Disturbances are widely recognised as key factors influencing the structure of plant communities, soil microbial activity, and therefore the N cycle (Pourreza et al. 2014; Bond et al. 2005). Given that some invaders may alter disturbance regimes, they may indirectly modify the N cycle.

Fire is one disturbance that may change upon invasion (Rabitsch et al. 2017). Invasive plants may alter the quality and quantity of fuel load and therefore the frequency and intensity of fires (Levine et al. 2003; D’Antonio 2000). Altered fire regimes may trigger a myriad of cascade effects on the structure and function of the ecosystem, including changes in the N cycle. The combustion of the organic matter (biomass, litter, or soil organic matter) represents a sudden mineralisation, that is, the liberation of mineral forms of N and other nutrients (paths 6, 9, and 13 in Fig. 4.1). Part of this inorganic N may be lost to the atmosphere as N oxides or leached by water runoff. The inorganic N remaining in the soil after the fire may be easily taken up by the first pioneer plants able to establish after the fire, which may include non-native opportunistic species. Therefore, an increased fire frequency by non-native plant invasions may increase the net loss of N from the ecosystem, accelerate the N fluxes, and change the balance between labile inorganic N and more durable organic N. Unfortunately, most studies reporting changes of the fire regime upon plant invasions (Rabitsch et al. 2017) do not directly address the impacts on the N cycle.

Changes of fire regime may also have indirect consequences on the N cycle. A remarkable example is that of the African grasses introduced in Hawaii, which promoted fire and declined native populations of fire-sensitive trees, such as *Metrosideros polymorpha*. The litter of this native tree is home to non-symbiotic N_2-fixing bacteria, which in turn do not develop in the litter of non-native grasses. Consequently, this change in the plant community leads to a reduction of N_2 fixation and therefore a decrease in N content in the invaded soils (Ley and D'Antonio 1998).

Certain non-native species may cause biotic disturbances previously absent in the recipient ecosystem. One such case is the wild boar, *Sus scrofa,* introduced in South America for hunting purposes. To obtain food, wild boars overturn extensive areas of soil, leaving behind areas bare of vegetation. In the Monte Desert biome of Argentina, the wild boar was found to enhance N mineralisation, probably because of increased soil moisture and oxygenation and the incorporation of litter into the soil (Cuevas et al. 2012). The increased mineral N and decreased vegetation cover may lead to a higher loss of soil N by runoff or volatilisation.

4.2.4 Alterations Caused by Changes in the Trophic Structure

Changes in the uppermost level of a trophic pyramid may have ecosystem effects disproportionate to the amounts of biomass involved. Animal invasions are particularly disruptive in oceanic islands, where the lack of certain trophic groups makes some species particularly vulnerable to introduced non-native species (Vitousek 1990). Addition of pigs, goats, or cattle on islands lacking large herbivores may lead to a catastrophic decline of primary producers. Given that plants are responsible for a great part of mineral N uptake from the soil, a drastic reduction of plant biomass will dramatically decline the proportion of N moving between the soil and the living organisms. The reverse effect may occur when a non-native predator is introduced to an island that has previously lacked predators capable of declining the populations of herbivores. Unfortunately, these types of studies rarely document impacts on the N cycle.

Invasion of non-native organisms belonging to existing trophic levels may also alter the N cycle by unbalancing the trophic structure. For instance, formerly glaciated regions of the northeastern United States have few native earthworm species, so the invasion of Asian earthworms decreased soil organic matter and increased N fluxes (Burtelow et al. 1998). The golden apple snail, *Pomacea canaliculata*, dramatically decreased aquatic plant populations in wetlands of Southeast Asia, which led to the dominance of planktonic algae, increasing N in water (Carlsson et al. 2007). The inordinate proliferation of the non-native freshwater mussels *Dreissena polymorpha* and *D. bugensis* in Lake Erie (USA) increased the ammonia excretion rate and reduced N turnover time (Conroy et al. 2005). The worldwide invader, the Pacific oyster, *Crassostrea gigas*, can establish dense populations that monopolize shorelines. In a field experiment, this species increased total oxidized N in the sediment and NH_4^+ in the pore water (Green et al. 2012). In a Spanish floodplain wetland, the extreme proliferation of the benthic omnivorous American red swamp crayfish, *Procambarus clarkii*, reduced the submerged vegetation and periphyton-grazing snails. As a consequence, N previously bound to sediments passed to the water column, becoming available for algae (Angeler et al. 2001). A similar effect is caused by the common carp, *Cyprinus carpio*, a fish invasive worldwide.

4.3 Are There General Trends on the Impact of Invaders on the N Cycle?

The diversity of impacts reported by different case studies (see Table 4.1) raises the question of whether there is a prevalent type of impact upon invasion by non-native species. This question began to be addressed for plant communities at the beginning of the twenty-first century and still continues to be explored, thanks to the growing number of studies available in the literature. The first major review was performed by Ehrenfeld (2003), who identified 79 papers comparing pools and fluxes of N, C, and water under non-native plants and under co-occurring or displaced natives. Ehrenfeld (2003) followed a vote-counting approach where, for each selected variable, the direction, but not the magnitude, of the change was noted. The main generalisations emerging from this seminal study were that invasive non-native species, as compared with associated natives, tend to have higher standing biomass and primary production; to produce litter that decays faster; and have soils beneath them that tend to have higher mineralisation rates and microbial N mass than noninvaded soils.

The publication of additional studies and the development of meta-analytical techniques allowed Liao et al. (2008) to revisit Ehrenfeld's conclusions. Using 94 studies, they quantified the changes of C and N pools and fluxes as the ratio of the mean value of a concerned variable in the invaded and in the uninvaded ecosystem. Moreover, this study posed the question of how impacts vary depending on the attributes of recipient ecosystems (forest, grassland, or wetland) and of the invaders (life form and N_2 fixation ability). This analysis confirmed most of Ehrenfeld's previous conclusions (i.e., plant invasion increases N pool sizes in plants, soils, and microbes, as well as primary production and rates of litter decomposition and soil N mineralisation). For most of the reported N pools and fluxes, the impact of woody and N-fixing invaders was greater than that of herbaceous and non-N fixing invaders, respectively. However, the impact was similar among forests, grasslands, and wetlands.

Three years later and using the same meta-analytical approach, a new synthesis of 199 articles on the impacts of non-native plants across different levels of ecological complexity, including variables related to the N cycle, was published (Vilà et al. 2011). Again, the question of how an attribute of the recipient ecosystems (island vs. mainland) and of the invaders (N_2-fixing ability) modulate the impact was addressed. Some of the reported impacts coincided with those previously described (increase of plant production and mineral N), but impacts on other variables did not significantly differ from zero (N mineralisation, litter decomposition). These discrepancies suggest that the variability of responses across studies is too great to derive generalisations. A small part of this variability was explained by the fact that N_2-fixing invaders increased N pools and N nitrification more than non-N_2-fixing invaders, but not by the insularity of the invaded ecosystem.

Pyšek et al. (2012) adopted a new approach to perform a global assessment of invasive plant impacts on the ecosystems by using classification trees. This tool allowed the authors to examine complex interactions among impact, the invaders' traits (those that might facilitate recruitment, competition and resistance to generalist herbivores), and environmental properties (the invaded region, biome, and habitat). Based on a total of 287 publications, this study found, among other results, that N content in plant tissues and soils, along with litter decomposition rate, were more often reported to increase than to decrease upon invasion. In contrast to previous studies, plant productivity was more often found to decrease. This study also revealed that taller species (>1.2 m) have more chances to impact plant productivity. Unfortunately, no pattern of plant traits and site characteristics was found for impacts on soil nutrient content.

The issue of the variability of impacts of plant invaders on the N cycle across studies was specifically targeted by a more recent meta-analysis (Castro-Díez et al. 2014). Based on 100 published articles and 345 case studies, the authors tested whether the impact size on N pools and fluxes depends on properties of the invaded site (disturbance, residence time, climate, insularity, or biome) or on functional and phylogenetic distinctiveness between the invader and the native species. This synthesis, along with previous ones, provided strong evidence that, overall, invasion by non-native plants increase total N pools and speed up N fluxes (Table 4.2). Again, a large variability of impacts across studies became evident, highlighting the relevance of the invasion context. Climate was found to be a relevant factor explaining variability: the invader's impact on N fluxes was greater under warm and moist conditions. This finding was attributed to the fact that the enzymatic reactions

Table 4.2 Number of case studies quantifying the impacts of plant invasions on the N pools and fluxes represented in Fig. 4.1 in four published meta-analyses

Pool/Flux	Code in Fig. 4.1	Liao et al. (2008)	Vilà et al. (2011)	Pyšek et al. (2012)[a]	Castro-Díez et al. (2014)
N-pools					
Plant/microbial biomass	10	49 (+)	–	60 (+)	47 (+)
Litter mass	3	–	–	–	54 (+)
Soil organic matter	5	83[b] (+)	26 (=)	–	36 (=)
Soil mineral N	7	88[c] (+)	47 (+)	436[d] (+)	45 (=)
N fluxes					
N_2 fixation	1	–	–	–	–
Litterfall	2	–	–	–	–
Litter decomposition	4	58 (+)	13 (=)	25 (+)	71 (=)
N mineralisation	6	58 (+)	11 (=)	–	23 (+)
Plant N uptake	8	42 (+)	90 (+)	105 (−)	69 (+)
N volatilization	9	–	–	–	–
N loss by runoff	11	–	–	–	–
Organic N uptake	12	–	–	–	–
Burning of biomass	13	–	–	–	–
Denitrification	14	–	–	–	–

The +, − or = sign in parentheses beside each figure indicates whether the variable measured in the invaded sites was on average greater, smaller, or not significantly different from the noninvaded sites

[a] This study only reports the number of cases where the variable was reported to increase or decrease upon invasion, with no statistical analysis to test whether any response was more frequent than the other. We show the most frequent response

[b] Number of case studies reporting soil carbon pool

[c] Number of cases reporting soil N pools, with no distinction between organic and inorganic N

[d] Number of cases reporting pools of any nutrient (not only N) on soils

involved in the N cycle are generally faster at higher temperatures, particularly if water availability is not limiting. This study also found stronger impacts on N pools when the invasive plants were N_2 fixing, tall, annual, or deciduous and the natives possess the reverse traits, according to the classic hypothesis that invaders that are functionally more different from natives have greater impacts on ecosystem properties (Chapin et al. 1996; D'Antonio and Corbin 2003). Other tested factors (residence time, whether the study was experimental or observational, or if the impact was mediated by disturbance) failed to explain impact variability, perhaps because some of them have effects only at a local scale.

Overall, considering several hundred field studies, the general trend of non-native plants to increase N pools and accelerate N fluxes within the ecosystem is strongly supported. Yet, there is also strong evidence of the wide variability and context dependency of the impacts. Finally, there is insufficient knowledge to derive general trends of how invaders alter the net ecosystem gains and losses of N (solid and double-dahsed arrows in Fig. 4.1).

4.4 Limitations of Current Knowledge and Future Research

The best knowledge we have so far on the impacts of non-native species on the N cycle is based on the syntheses of published field studies. But does this information reflect what happens in nature? Several authors have warned about the tendency of scientists to select case studies where dramatic impacts are more likely (Levine et al. 2003; Hulme et al. 2013). In fact, Castro-Díez et al. (2014) found that N_2-fixing species (those with higher potential to alter the N cycle) accounted for 21 % of the 345 reviewed case studies, although the average proportion of N_2-fixing invaders across different databases worldwide is 15 %. Hulme et al. (2013) highlighted that only a small proportion of non-native plants causing impacts worldwide have been the target of robust quantitative assessments and that scientists tend to select species already studied. Accordingly, only 9 and 12 species accounted for one-third of the case studies reviewed by Hulme et al. (2013) and by Castro-Díez et al. (2014), respectively. The selection of variables accounting for impacts on the N cycle is also biased. On average, impacts on N pools are more studied than impacts on fluxes. Only 3 of the 10 N fluxes of Fig. 4.1 (litter decomposition, N mineralisation, and plant N uptake) were covered by any of the four syntheses (Table 4.2). Terrestrial ecosystems have been explored much more frequently than aquatic ecosystems in the available reviews. Only Liao et al. (2008) explicitly included impacts on wetlands, but the number of case studies was only 5 % to 17 % of the total (table S2 of Liao et al. 2008). Castro-Díez et al. (2014) specifically targeted terrestrial ecosystems, and Vilà et al. (2011) and Pyšek et al. (2012) were not explicit about the inclusion or non-inclusion of aquatic ecosystems. Finally, we are not aware of any review addressing the impacts of non-native animals on the N cycle. Therefore, to have a complete and unbiased picture of the overall impacts of invasions on the N cycle, future research should explore the impacts of non-native animals, address more N-cycle variables (particularly net ecosystem gains and losses of N, see Table 4.2 and Fig. 4.1, solid and double-dashed arrows), and include more case studies from aquatic ecosystems.

From an applied perspective, a relevant challenge to prioritize the management of non-native species at a particular site is to know whether the impact of non-native species can be predicted from the knowledge of previous impacts in other sites, or even from other regions. Evidence suggests that impacts of the same species may largely vary in magnitude and even in direction across different contexts. Part of this variation may be explained by climatic factors and by the functional novelty of the invasive species, but another great part of the variation is the result of local and historical factors, such as community structure, soil properties, disturbance, or residence time. Hulme et al. (2013) demonstrated that the variability of a given impact increases with the number of studies, and emphasised that results from single studies at single locations or years might not be widely generalisable. Unfortunately, according to the data collected by Castro-Díez et al. (2014), the number of invasive species in which the impacts on the N cycle have been quantified several times by independent studies in different locations is very low. In summary, in addition to increasing the number of explored species, variables and ecosystem types, more information is needed on the impacts of the same species across different sites and times.

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Chapter 5
Hydrological Impacts of Biological Invasions

Jane A. Catford

Abstract The quantity and distribution of freshwater are fundamental to many ecosystem services, including water supply, flood attenuation, habitat provision, electricity generation, navigation, and recreation. Non-native plants and animals can degrade hydrological functions through their physiology, morphology, behaviour, and interactions with other species, which can be compounded when non-native species are ecosystem engineers or transformers. Using the hydrological cycle and drawing on key global examples, this chapter outlines seven main ways in which non-native species can disrupt hydrological services and how these impacts can be managed. Non-native plants may alter local and regional climates by modifying land–atmosphere transfers of heat and moisture, surface roughness and albedo, and concentrations of aerosol particles. Differences in native and non-native water use can alter catchment runoff (usually reducing water yield), especially when non-native vegetation covers extensive areas (e.g., mesquite and eucalypts). Non-native plant invasion may alter the seasonal availability of water because of differences in the timing and duration of water use (e.g., deciduous natives vs. evergreen invaders). Non-native animals and plants can change ground surface and soil characteristics, altering surface and subsurface flows, infiltration rates, and water residence times (e.g., earthworms and beavers). Species that invade wetlands, lakes, and rivers can trap sediment, narrowing flow channels and reducing flood attenuation (e.g., tamarisk, *Sagittaria*, mimosa). Some plant growth forms and animal behaviours can cause channel collapse, increase sediment erosion, and alter flow paths (e.g., willows, coypu). Non-native species can modify water passage and flow velocities by

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altering geomorphology and hydraulics (e.g., *Salvinia*, zebra mussels). Invasive species management remains difficult because of feasibility and conflicting values of species (e.g., ecology versus economy, upstream versus downstream effects). An ecosystem services framework may help reconcile the differential impacts that non-native species have in time, space, and on the delivery of various services.

Keywords Catchment • Ecosystem engineer • Flood • Habitat provision • Hydrological cycle • Land use • Water supply

5.1 Introduction

Hydrological services relate to the supply and regulation of freshwater and have an estimated value exceeding US $2.8 trillion per annum (Costanza et al. 1997). The timing and magnitude of runoff, flooding, and groundwater recharge are fundamental to many ecosystem services. To optimise the supply of some of these services (e.g., navigation, water supply, and hydropower), the hydrological cycle has been modified though the construction of dams, channelisation and diversion of rivers, and transformation of river floodplains. Changes in land use, increases in water storage capacity and extraction, flow stabilisation, and loss of wetlands have affected hydrology and the regulation of freshwaters. Currently, global freshwater use exceeds long-term accessible supplies by as much as 25 %, made possible through overuse of groundwater and interbasin water transfers (i.e., between catchments / watersheds). Such actions have increased the availability of some services, but they have reduced the availability of others, including services in other times and locations.

Although less dramatic than massive engineering works that transform river ecosystems, biological invasions can compromise and threaten hydrological services. By changing land cover, water use, geomorphology and hydraulics, non-native plants and animals can alter the quantity of water and its distribution in time and space. The relative importance of invasion-induced changes to hydrology is likely to increase as the demand for, and scarcity of, hydrological services intensifies as a result of human population growth and global environmental change (Costanza et al. 1997; Millenium Ecosystem Assessment 2005- MEA 2005 hereafter; Vörösmarty et al. 2010). Compounding these trends, biological invasions are increasing in both number and impact, and will likely further stretch an already overextended system. Understanding, managing, and ameliorating negative effects of non-native species on hydrology is therefore crucial.

Based around the hydrological cycle, and drawing on key examples from across the world, this chapter outlines seven main ways in which non-native species invasions can disrupt hydrological services and how these impacts can be managed. Although hydrological services are integrally linked with services that relate to water quality, soil formation, nutrient cycling, and waste treatment, the focus of this chapter is on the supply and regulation of freshwater. Examples are restricted to non-native animals and plants, reflecting the focus of research conducted to date, but it is important to note that disease and pathogens can also affect hydrological services (Strayer 2010).

5.2 What Are Hydrological Services and How Are They Provided?

Hydrological services relate to the supply and regulation of freshwater, particularly its quantity and availability in time and space. Hydrological services can be divided into four categories: (1) supporting services that support ecosystems, biota, and other types of ecosystem services; (2) provisioning services that relate to water as a resource itself, whether it is used on- or off-site; (3) regulating services that encompass the role of water in mitigating damage to human life and property; and (4) cultural services, which include the spiritual, social, and aesthetic values of freshwater environments (Table 5.1).

The distribution and amount of water in a landscape is driven by the hydrological cycle (Fig. 5.1). Falling as precipitation, freshwater can be intercepted by vegetation and cloud cover before reaching the ground. Upon reaching the ground, water can directly contribute to surface runoff or can infiltrate the soil, contributing to subsurface and groundwater storage and flows. Water can evaporate from all storages, and may be transpired back to the atmosphere by plants. Water can reach river channels and water bodies directly from precipitation or through surface runoff, subsurface flows, and base flows, with the speed of water flow generally declining in that order. The length of time that water spends in a particular flow path or storage is called its residence time. Shorter residence times reflect that a volume of water is conveyed over a shorter period of time, resulting in shorter floods with higher peaks that come soon after a rainfall event. Once in a water body or watercourse, water may be stored, evaporated, used by organisms, or may flow to downstream coastal ecosystems.

For the provision of ecosystem services, it can help to either maintain or disrupt the natural hydrological cycle. The hydrological cycle is often disrupted to ensure the optimal provision of some hydrological services (e.g., continual access to a steady flow of water for irrigation) (Catford et al. 2011). Even though the total amount of water in the cycle remains the same, such modification alters the balance of water amongst the various storages and flows. Changes to the storage or flow of water at any point in the cycle will therefore affect water regulation and the hydrological services of the entire catchment. Although seemingly less radical than overall changes in water quantity, changes in the temporal and spatial characteristics of water availability can have a larger effect on service provision as many hydrological services rely on the consistency of water access and supply.

Table 5.1 Hydrological services grouped into four major categories with examples of non-native species impacts

Hydrological services		Non-native species impacts
Supporting services	Water, nutrients and sediment for other ecosystems	North American beavers can transform the structure and function of entire ecosystems by altering the physical, chemical, and geomorphological characteristics of rivers and riparian zones. Impacts include higher rates of erosion by converting forests to meadows; increases in nutrient availability from wood debris in waterways, leading to increases in primary productivity and changes in invertebrate assemblages; dams acting as barriers to dispersal and indirectly changing water temperature; indirectly facilitating other non-native species that are better suited to the modified environmental conditions than native species (Lizurralde et al. 2004; Anderson et al. 2009; ISSG 2015).
	Habitat and dispersal vector for biota	
Provisioning services	Transport and navigation	Zebra mussels clog water intake screens and pipes of municipal water supplies and hydroelectric companies, degrade the quality, taste, and odor of potable water, and can lead to bioaccumulation of organochlorine and heavy metals in fish and ducks that prey on them (Pejchar and Mooney 2009).
	Waste removal and dilution	
	Hydroelectricity generation	
	Freshwater products (e.g., fish)	
	Municipal, industrial, agricultural, commercial water use	
	Thermoelectricity generation	
Regulating services	Flood attenuation	Dense populations of submerged and floating macrophytes (e.g. salvinia, Eurasian water-milfoil) increase flood risk by reducing flow velocities and water passage, and increasing rates of sedimentation and reducing rates of erosion (Strayer 2010).
	Drainage	
	Saltwater intrusion	
	Sedimentation and erosion	
	Dryland salinisation	
Cultural services	Spiritual and religious	The diatom didymo or rock snot (*Didymosphenia geminata*) has impeded the recreational, tourism, and aesthetic value of invaded rivers in New Zealand (ISSG 2015). The whole South Island of New Zealand was declared a controlled area in 2005 requiring that all equipment (boats, fishing gear, clothes) used in an infected waterway must be cleaned before use in another waterway.
	Education	
	Tourism	
	Recreation	

Refer to Table 5.2 for more examples (MEA 2005; Brauman et al. 2007)

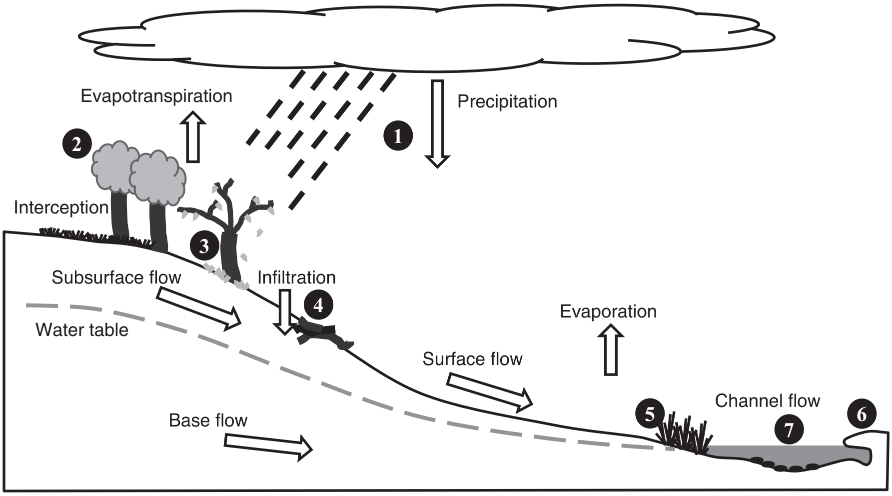

Fig. 5.1 Hydrological cycle showing the seven main ways that non-native species impact the quantity and regulation of freshwater. Features marked by *numbers* relate to impacts described in Table 5.2: (*1*) local and regional climate; (*2*) water use (trees vs. grass); (*3*) seasonality of water use (evergreen vs. deciduous trees); (*4*) ground surface and soil texture modification (tree branches altering surface flow); (*5*) wetland encroachment, channel narrowing, and sedimentation (macrophytes on channel edge); (*6*) destruction and erosion of channel form (mammal burrow undercutting riverbank); and (*7*) channel water flow (bivalves armouring channel)

5.3 Ways in Which Biological Invasions Disrupt Hydrological Services

Invasion impacts are defined as a measurable change in the state of an invaded ecosystem that can be attributed to non-native species (Ricciardi et al. 2013). Non-native species impact hydrology through changing the amount, location, and seasonality of water use, and through changes to the physical environment, which affect patterns, volumes, and velocities of water flow. As well as these direct effects, non-native species can indirectly alter the quantity and regulation of water through their interactions with other species, including native biota, and through feedback effects on local and regional climates. There are seven main ways in which species can alter hydrology and the hydrological cycle (Table 5.2; Fig. 5.1): the first two mechanisms relate to water quantity and the remaining five mechanisms affect water regulation. These mechanisms are not mutually exclusive and many of them co-occur.

Table 5.2 Seven main ways that non-native species can affect the quantity and regulation of water, mechanisms through which they do so, and likely impacts on the hydrological cycle

Invader effects	Mechanisms of impact	Impacts on hydrological cycle	Species characteristics	Examples
Water quantity				
(1) Local and regional climate	Non-native plants change surface roughness, temperature and albedo, and land–air transfers of heat and moisture	Indirect, cumulative changes to precipitation and evaporation in catchment	Different structural form to native vegetation; high transpiration rates; darker foliage	Invasion of grasslands and heathlands by non-native trees
(2) Water use	Non-native plant populations increase interception and evaporation because of differences in their morphology, structure and population densities compared to native species	Increased evapotranspiration and water storage in plants; greater portion of water intercepted by vegetation aboveground and immediately evaporated; lower runoff	Novel life forms change vegetation structure; low intraspecific competition allows species to reach high densities	Pasture grasses; giant reed, *Arundo donax*; non-native trees
	Per capita water use of non-natives differs from natives because of their life stage (young plants use more water), growth rates or photosynthetic pathway (C3 plants use more water than C4 and CAM plants)	Differences in water use alters runoff, especially during plant growth season	Short life spans; rapid population growth; age distribution of population (e.g., dominance of juveniles); photosynthetic pathways	Blue gum, *Eucalyptus globulus*
	Non-native plants have greater access to soil moisture and groundwater than native plants	Lowers water table; reduces aquifer recharge, groundwater storage and base flows	Deep roots; expansive root system; high root biomass; novel life form (e.g. tree in heathlands)	Tamarisk; mesquite, *Prosopis* species; mimosa; pines; wattles, *Acacia* species
	Non-native animals and pathogens reduce biomass and productivity of native vegetation	Lower water use, interception and evapotranspiration increase water availability and decrease water residence time; higher flood risk	Herbivores that reduce vegetation productivity	Rabbits and other terrestrial herbivores

Water regulation				
(3) Seasonality of water use	Timing of growth of non-native plants differs from native plants	Seasonal changes in water availability	Different growth season to native plants (e.g., C3 vs C4 and CAM plants, deciduous vs. evergreen)	Willows and poplars in Australia; yellow star thistle, *Centaurea solstitialis*, in USA
(4) Ground surface and soil texture modification	Non-native species change physical structure of ground and infiltration capacity of soil	Changes to runoff flow paths and velocities; changes in surface water ponding and infiltration location and rates; changes in water residence time, storage and flows	Plants: distinct from natives in type and amount of biomass, chemical composition and amount of litter, dead wood, root structure, root biomass, and timing of leaf senescence	Plants that differ in structure or biomass from native vegetation
			Animals: behavior related to burrowing, digging; soil-dwelling invertebrates	Animals: earthworms, including common earthworm, *Lumbricus terrestris*; rabbits
(5) Wetland encroachment, channel narrowing and sedimentation	Non-native plants trap sediment and encroach channels, wetlands and floodplains	Reduces flood attenuation and water residence times; alters hydraulics, flow paths and velocities; results in flashier hydrographs, faster runoff, and increased flood risk; impedes navigation	Plant structure and morphology that reduces flow speeds and traps sediment; plastic or variable growth form; capacity for clonal spread	Tamarisk; mimosa; giant reed, *Arundo donax*; sagittaria; common reed, *Phragmites australis*
(6) Destruction and erosion of channel form	Growth form of plants and behavior of animals can cause channel collapse, sediment erosion and change flow paths	Altered channel morphology, sediment size and hydraulics changes patterns and velocities of water flow	Plants: different root structure and morphology from natives.	Plants: willows and poplars
			Animals: burrowing, dam building, benthic feeders.	Animals: pigs; carp; beavers; coypu, *Myocastor coypus*; Chinese mitten crab, *Eriocheir sinensis*

(continued)

Table 5.2 (continued)

Invader effects	Mechanisms of impact	Impacts on hydrological cycle	Species characteristics	Examples
(7) Channel water flow	Non-native species clog waterways and infrastructure	Slows and impedes water flow; increases water pondage; impedes navigation and hydropower production	Plants: floating or submerged plants that can form dense stands (often monocultures); clonal; rapid population growth	Plants: salvinia; water hyacinth; Eurasian water-milfoil
			Animals: habitat-forming	Animals: bivalves
	Non-native bivalves armour channel	Reduction in channel roughness increases flow velocity, reduces storage times, and increases flood risk downstream	Bivalves with hard surfaces	Freshwater mussels, e.g., zebra mussel and quagga mussel from *Dreissena* genus
	Grazing by non-native animals reduces abundance of aquatic macrophytes	Reduces channel roughness; increases erosion, sediment suspension and transport; results in increased flow velocities, flashier hydrographs, and increased flood risk downstream	Voracious herbivores	Carp; coypu, *Myocastor coypus*; golden apple snail, *Pomacea canaliculata*; rusty crayfish, *Orconectes rusticus*

Changes in water quantity mostly affect supporting and provisioning services, whereas changes in water regulation mostly affect provisioning and regulating services. Cultural services can be affected by any change depending on the human values of a given system. Characteristics of non-native species that may be linked with species impacts on hydrology are noted (some hypothesised, some observed), along with some iconic examples where they exist. Water regulation refers to the distribution and flows of water in space and time. Refer to ISSG (2015) for authorities of species names. Table compiled using information from: Holdsworth and Mark 1990; Calder and Dye 2001; MEA 2005; Charles and Dukes 2007; van Wilgen et al. 2008; Deo et al. 2009; Pejchar and Mooney 2009; Ehrenfeld 2010; Vilà et al. 2010; ISSG 2015 and references there in

5.3.1 Local and Regional Climate

Non-native plants can change evapotranspiration rates, local temperatures, surface roughness, concentrations of aerosol particles, and surface albedo by modifying the characteristics of vegetation and land cover. Most research about the effects of vegetation on climate has focused on vegetation clearing, but increases in vegetation biomass, especially of woody vegetation with high evapotranspiration rates, may alter local and regional rainfall patterns by changing transfers of heat and moisture between the land and atmosphere (van Dijk and Keenan 2007). Although further research is required to ascertain relationships between vegetation and local rainfall (Vanclay 2009), large expanses of non-native trees could change the amount and seasonality of rainfall in an area by increasing (1) the amount of water stored in the air and atmosphere, (2) surface roughness, and (3) concentrations of aerosol particles, which provide condensation nuclei. Despite the potential for increased precipitation, increases in tree abundance will still typically result in lower water yields (the amount of water remaining after evapotranspiration) locally as well as regionally (van Dijk and Keenan 2007).

5.3.2 Water Use

The most commonly cited impact of biological invasions on hydrology is through the increased use of water by non-native plants (Charles and Dukes 2007; van Wilgen et al. 2008). Although riparian and instream plant use can increase, the greatest effects on water quantity are brought about by non-native vegetation that covers extensive areas of catchments where the majority of runoff is produced (Calder and Dye 2001; MEA 2005). Woody shrubs and trees that have invaded South Africa have reduced the water yield from upland fynbos ecosystems by 30 % (and national runoff by 7 %) (van Wilgen et al. 2008), with an estimated annual cost of US$68 million (Charles and Dukes 2007). Tamarisk (also known as salt cedar), *Tamarix* spp., has exerted similar impacts in the southwestern USA, where tamarisk trees consume 1.4–3.0 billion m^3 more water than native riparian species (Pejchar and Mooney 2009). Subsequent changes to water supply, hydropower generation, and flood risk are estimated to cost US$133–285 million per annum (Charles and Dukes 2007). Woody species belonging to the genera *Pinus*, *Eucalyptus*, *Acacia*, *Prosopis*, and *Tamarix* are thought to exert such impacts because their deep roots enable them to access soil moisture and groundwater that native vegetation cannot (Pejchar and Mooney 2009). However, such effects are not limited to woody species. Invasion of the yellow star thistle, *Centaurea solstitialis*, into annual grasslands of the western USA has increased summer water use by 105–120 mm per annum (Levine et al. 2003). Similarly, conversion of native tussock grasslands to non-native pastures in upland areas of New Zealand has halved yearly runoff volumes (Holdsworth and Mark 1990).

Non-native plants can reduce water yields by increasing interception, evapotranspiration, and water storage in plant tissues through higher biomass, productivity, evapotranspiration rates, and leaf area indexes, and because they add or change the structural complexity of vegetation (Pejchar and Mooney 2009). Grasslands converted to forest have resulted in a 45 % average reduction in stream flow (Brauman et al. 2007), and tamarisk can increase annual evapotranspiration by 300–460 mm (Levine et al. 2003). One of the reasons for higher water yields in tall tussock (bunch) grasslands in New Zealand compared with non-native-dominated forest and pasture ecosystems is attributed to the anatomy of the native tussock leaves where transpiration is minimised and water droplets are intercepted from fog (Holdsworth and Mark 1990). Plants that photosynthesize using the C3 pathway typically use more water than C4 plants, which use more water than CAM plants. Young plants use more water than mature plants because of their faster growth rates, so when new populations of non-native plants invade and colonise an area, water use will be particularly high (Brauman et al. 2007).

Invasion may not always lead to declines in runoff, however. Non-native grasses that have invaded the midwestern USA have shallower roots than the native perennial grasses that they have replaced, potentially reducing water use (Pejchar and Mooney 2009). Non-native animals have a negligible direct effect on water quantity but can affect plant water use through herbivory and by altering species composition (Ehrenfeld 2010).

5.3.3 Seasonality of Water Use

Non-native plants that differ in phenology to native plants may alter the seasonal availability of water because of differences in the timing and duration of water use (Levine et al. 2003; Ehrenfeld 2010). For example, non-native annual grasses in California transpire for a short period in late winter and spring, whereas native perennial grasses also transpire in summer (Levine et al. 2003). The invasion of evergreen plants in areas formerly dominated by deciduous, or seasonally dormant, plants (e.g., non-native evergreen trees into seasonally dormant South African grasslands; van Wilgen et al. 2008) and vice versa has resulted in seasonal changes in water use that reflect plant phenology. C4 and CAM plants are predicted to increase in abundance with climate change because they are more tolerant of warmer and drier conditions than C3 plants. Although the hydrological impact of these predicted changes in vegetation will likely be dwarfed by the changes in climate that facilitate them, seasonal shifts in water uptake are likely to occur.

5.3.4 Ground Surface and Soil Texture Modification

Non-native animals and plants can alter the physical features of the ground surface and soil, altering surface and subsurface flows, infiltration rates, soil bulk density and water-holding capacity, and water residence times. The physical structure of plants can affect patterns of water flow and local storage, but plants can also affect soil texture and organic content, and their decomposed roots can provide passages for subsurface water flow. Animals that burrow, dig, or live in the soil can similarly alter surface and subsurface storage and flows. The European earthworm, *Lumbricus terrestris*, highly invasive in temperate and boreal regions of North America, changes the structure of the soil by creating permanent vertical burrows in the mineral layer and increasing soil porosity and bulk density (Invasive Species Specialist Group 2015) (ISSG 2015 hereafter). As well as altering river hydrology, hydraulics, and geomorphology through dam construction, the non-native beaver, *Castor canadensis*, reduces riparian forest cover in southern South America where individuals forage as far as 120 m from rivers (Anderson et al. 2009). Deforestation by beavers in Chile and Argentina has increased erosion because of exposed slopes (Lizurralde et al. 2004) and has effectively converted closed southern beech, *Nothofagus*, forest to grass and sedge meadows, which are often dominated by non-native herbs (Anderson et al. 2009; ISSG 2015).

5.3.5 Wetland Encroachment, Channel Narrowing, and Sedimentation

Terrestrial non-native plants can invade wetlands and floodplains, especially if natural flooding has declined (Catford et al. 2011), trapping sediment and reducing their capacity to absorb and attenuate floods. Wetland plants can encroach water channels, slowing water velocities and facilitating sedimentation. Originally from the southern USA, the aquatic macrophyte *Sagittaria platyphylla* invades wetlands and drainage, irrigation, and river channels in southeastern Australia (Catford et al. 2011). Growing in water about 0.3 m deep, the emergent form of the plant spreads clonally via stolons, which extend out into water depths as great as 1.5 m where it grows in its submerged form. As sediment accumulates over time, the species is able to gradually spread out into the main river channel, diverting, slowing, and impeding water flow (Fig. 5.2). The giant sensitive tree, *Mimosa pigra*, also reduces water flow and increases silt levels in rivers (ISSG 2015). Tamarisk species are estimated to cost US$53 million per annum because of channel narrowing (Pejchar and Mooney 2009).

Fig. 5.2 (**a**) *Sagittaria platyphylla* encroaching on a tributary of the River Murray, Victoria, Australia (emergent form visible) with (**b**) submerged form spreading into deeper water via stolons from emergent plants (Photographs by Jane A. Catford)

5.3.6 Destruction and Erosion of Channel Form

The growth form of plants and behaviour of animals can cause channel collapse and sediment erosion, and can change flow paths. Burrows of the South American coypu, *Myocastor coypus*, introduced into North America, Europe, Africa, and Asia, undermine riverbanks and embankments. Coypu further increase channel instability and erosion by eating plant roots and rhizomes (ISSG 2015). In Australia, non-native willow trees, *Salix* spp., can modify banks and obstruct and divert stream flow with their dense growth above and below ground.

5.3.7 Water Movement in Channel

Non-native species can modify flow dynamics by altering the morphology and hydraulics of waterways. Prolific growth of non-native plants and bivalves can block channels and infrastructure, impeding water movement, navigation, waste disposal, and hydropower generation, as well as affecting water quality and providing suitable conditions for mosquito breeding (Pejchar and Mooney 2009). Submerged and floating macrophytes (e.g., salvinia, *Salvinia molesta*; water hyacinth, *Eichornia crassipes*; Eurasian milfoil, *Myriophyllum spicatum*; and American elodea, *Elodea canadensis*) are among the worst weeds in the world (ISSG 2015). Their dense growth reduces water speed, deepens channels, increases sedimentation rates, reduces erosion rates, and increases flood risk (Strayer 2010). In the Hudson River in the northeastern USA, the floating European water chestnut, *Trapa natans*, reaches densities ten times that of the native American eelgrass, *Vallisneria americana*, which it has replaced, thereby reducing water flows, impeding river access, and negatively impacting recreation and native animals (Strayer 2010). North American beavers, invasive in Europe, Russia, and South America, directly alter the flow dynamics of rivers, with marked effects on water movement and flood risk (ISSG 2015).

The globally invasive zebra mussel, *Dreissena polymorpha*, blocks pipes and other infrastructure (Pejchar and Mooney 2009), but their hard surfaces can effectively armour channels too, potentially increasing water velocities in wider channels. In some systems, water velocities and flow increase following a reduction in native plant densities. Grazing by golden apple snails, *Pomacea canaliculata*, in southeast Asian wetlands and rusty crayfish, *Orconectes rusticus*, in North American rivers has reduced the density of macrophytes. New Zealand mudsnails, *Potamopyrgus antipodarum*, can reach population densities of tens to hundreds of thousands of individuals per square metre and can consume up to 75 % of gross primary production (ISSG 2015).

5.4 Feedbacks Between Hydrological Modification and Invasions

Animals, and particularly plants, clearly affect hydrology and water regulation through their morphology, physiology, and behaviour (albeit inconsistently; Vilà et al. 2010), but this is not a one-way relationship. The hydrological characteristics of an ecosystem are necessarily a strong determinant of the resident biota because of organism behavioural and ecophysiological requirements. Native species may have adapted to the historical hydrological characteristics of their ecosystem, so hydrological modification can prompt a decline in their abundance and vigour, and may directly or indirectly facilitate invasion (Catford et al. 2011). Evidence suggests that hydrological modification has led to a decline in the abundance of native plants in River Murray wetlands in southeastern Australia, which has subsequently facilitated invasion by less specialised non-native species (Catford et al. 2011).

Ecosystems with modified hydrology seem particularly susceptible to invasion by non-native species, which may then go on to alter hydrology further (Strayer 2010). Species that alter environmental conditions in their favour are referred to as ecosystem engineers (animals) or transformers (plants). Beavers and zebra mussels are obvious examples, as is *Sagittaria* in that it facilitates sedimentation, which then provides more habitat suitable for its colonisation and spread (Fig. 5.2). In some cases, it can be difficult to ascertain whether invaders are drivers, passengers, or transformers of environmental change (Lindenmayer et al. 2015). Such a situation is seen in the southwestern USA with the invasion of tamarisk along rivers. Although the majority of evidence seems to imply that tamarisk is a passenger of hydrological modification because it is able to reach groundwater that native woody species cannot, tamarisk has probably exacerbated hydrological change by lowering water tables further (Stromberg et al. 2007; Ehrenfeld 2010). In terms of management, it is important to determine whether invasion promotes a change in hydrology or whether hydrological modification facilitates invasion. Transformers and ecosystem engineers often require simultaneous species and environmental control because of the positive feedback between invasion and environmental change (Lindenmayer et al. 2015).

5.5 Managing Invasion Impacts on Hydrological Services: Can the Concept of Ecosystem Services Help?

Non-native species can disrupt hydrological services, but the perception of such changes can vary, with some changes perceived as positive and others as negative (Pejchar and Mooney 2009; Pyšek et al. 2012). In areas where deforestation has led to salinisation, non-native trees with deep roots and high rates of evapotranspiration may help alleviate negative effects of salinisation by lowering water tables. However, deep-rooted trees that lower water tables and deplete groundwater reserves are highly undesirable in formerly treeless areas (Brauman et al. 2007). Non-native species that trap sediment can be perceived as harmful in some situations (Fig. 5.2), but they can also help to counteract bank destabilisation and elevated rates of erosion that may be the result of independent changes in land and water use (Pejchar and Mooney 2009). Such tradeoffs are not restricted to ecosystem services that relate to freshwater.

Conflicts between non-native species (often negative) impacts on ecology versus their (often positive) impacts on society and the economy are keenly felt and difficult to reconcile (van Wilgen et al. 2011). First introduced to India in 1857, mesquite, *Prosopis juliflora*, was actively planted in the nineteenth and twentieth centuries and now occurs throughout the arid and semi-arid regions of the country (Tewari et al. 1993), where it has increased water use, dramatically decreasing catchment runoff (Fig. 5.3). Deliberate plantings of wattle, eucalypt, and pine species have culminated in similar effects. Reducing the abundance of these species would improve water security, especially in downstream ecosystems, but it would come at a marked cost to local communities that have come to rely on these species for timber, fuel, and other products. Mesquite accounts for more than 70 % of firewood in rural parts of tropical arid and semi-arid India, and is also a major fuel source in urban areas (Shackleton et al. 2014), so its control would be met with

Fig. 5.3 (**a**) Impenetrable monoculture stands of mesquite, *Prosopis juliflora*, that extend over vast tracts of land in Punjab, northern India. (**b**) Local people harvesting mesquite timber in Tamil Nadu, southern India. (**c**) Dense stand of blue gum, *Eucalyptus globulus*, with an understory of gorse, *Ulex europaeus*, in Ooty, southern India. (**d**) Person collecting blue gum leaves to sell for oil production in Ooty. These two non-native tree species reduce catchment water supplies across India, but are valued for timber, seeds, oil, and other products (Photographs by Jane A. Catford)

resistance (Fig. 5.3). Quantifying the relative value of these different ecosystem services could potentially help to reconcile this conflict, provided that disadvantaged parties are appropriately compensated. However, quantifying the values of ecosystem services and the impacts of biological invasions is not easy.

Accurate assessment of the relative costs and benefits of non-native species and ecosystem services relies on (1) isolating the effects of non-native species from other factors that might affect ecosystem services; (2) quantifying the cost of different ecosystem services and ecological impacts in a single currency; (3) accounting for acute and chronic, onsite and offsite, and immediate and delayed effects of non-native species; and (4) predicting the likely value of ecosystem services and likely impacts of invasive species in the future such that appropriate discount rates can be applied.

Even with perfect knowledge, policy and management options might be limited. Jurisdictional boundaries can make enforcement and cooperation difficult, as costs and benefits to ecosystem services are often geographically displaced, especially when considering rivers and their catchments. Activities in the upper regions of the Mekong River catchment in China may be most felt in the five countries downstream, for instance. Even with support for non-native species control, effective approaches may be unavailable, especially in aquatic ecosystems. There has been some success controlling non-native plants (e.g., biological control of *Salvinia molesta* by the salvinia weevil, *Cyrtobagous salviniae*; ISSG 2015), but many control programs have been unsuccessful in freshwater ecosystems (Strayer 2010), no doubt hampered by access issues and restrictions on chemical use in aquatic environments.

One of the few examples of a highly coordinated national-scale approach to invasive species control is the Working for Water program in South Africa. With water demand outstripping supply in more than half of South Africa's water management areas, this innovative program was initiated by the national government in 1995 to alleviate both poverty and water stress: people were employed to cut down invasive woody species with the aim of reducing water use and restoring hydrological services (van Wilgen et al. 2008). Despite clearing 1.2 million hectares of non-native trees within the first 8 years of the program, much of the landscape is still dominated by invasive trees. This case study highlights the difficulties in controlling invasive species and keeping up with their rates of spread even when levels of support for control are high (van Wilgen et al. 2012).

5.6 Conclusions

The magnitude of non-native species impacts on water resources and hydrology is probably underestimated because of a lack of impact-based research (Pyšek et al. 2012), particularly at the ecosystem level (Ricciardi et al. 2013), and the difficulties of isolating invasion impacts from other impacts on hydrology. Nevertheless, there is ample evidence indicating that non-native species, especially plants that cover extensive areas, can have profound effects on hydrological services. Some of these species have become iconic case studies that have captured the attention of natural resource managers and policy makers. Despite this, water-demanding trees in South Africa and India, ecosystem-engineering invertebrates in North America, and habitat-transforming macrophytes in Asia and Australia have proved difficult to manage, which can reflect the conflicting values of the species and impediments to their control. Provided that certain challenges are met, the concept of ecosystem services may provide a framework for reconciling the differential impacts that non-native species have in time, space, and on the delivery of various services.

The limited success in controlling invasive woody species in South Africa, despite a control effort that could rarely, if ever, be matched, is sobering. Although biological control may be able to lessen impacts in some cases, the most effective way to prevent hydrological impacts of similar magnitudes is to identify and manage high-risk species, and the conditions that facilitate their invasion, ahead of time. Invasion ecology researchers appear to have embraced this need, as the escalating number of studies focusing on invasive species impacts, impact metrics, and impact-focused species traits attests. Ascertaining the cumulative effects of multiple non-native species, which could potentially be controlled collectively, will be important for optimising management efficacy.

As the demands for, and scarcity of, freshwater resources and hydrological services heighten (Costanza et al. 1997; Vörösmarty et al. 2010), and the likelihood and impacts of invasion increase, there will be increasing need for identifying, managing, and ameliorating the impacts of invasive species on the quantity and regulation of water.

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Part II
Impacts on Provisioning Services

Chapter 6
Decreases in Crop Production by Non-native Weeds, Pests, and Pathogens

Guillaume Fried, Bruno Chauvel, Philippe Reynaud, and Ivan Sache

Abstract The worldwide trade of agricultural products and high levels of disturbance and fertilisation make arable lands particularly vulnerable to biological invasions. Clearing for the development of arable land has been an unprecedented event that created a new and more homogeneous habitat which allowed many species to spread to become (sub)cosmopolitan weeds, pests, and pathogens. Through competition for light, water, and nutrients (weeds), or destruction of plant tissue (pests and pathogens), harmful organisms can potentially reduce crop yield by 10–40 % on average. Historically, some non-native species produced spectacular invasions and caused incalculable damage by annihilating crop production at large scales: for example, potato late blight, *Phytophthora infestans*, which was one of the factors causing the Irish Potato Famine, and the American vine phylloxera, *Daktulosphaira vitifoliae*, which devastated vineyards across the whole of Europe. Nowadays, it is estimated that non-native weeds, pests, and pathogens cause as much as US$248 billion in annual losses to world agriculture, making this the sector most affected by the introduction of non-native species. The use of pesticides has long protected crop yield satisfactorily. However, because of the undesirable side effects that may be associated with pesticide use (e.g., development of resistant biotypes and water pollution), more integrated approaches to combat invasive species are needed, including prevention (phytosanitary control) and cropping systems with higher potential for ecological regulation.

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6.1 Introduction

Since the development of agriculture during the Neolithic Period, a large number of crop species have been cultivated on arable lands to produce food or fibre. This new man-made environment has expanded continuously to amount to 1386 million ha, that is, 10 % of the world's land area. Cropland is particularly prone to biological invasions that proceed through the different steps of introduction, establishment, and spread. The introduction of crop species into new regions has concomitantly promoted the accidental introductions of many weeds (plants interfering with crops), pests, and pathogens strongly associated with the crops in their native range. In contrast to other unintentional pathways of introduction (e.g., soil or commodities, such as wool or wood), unintentional introduction of non-native weeds, pests, and pathogens with crop seeds or on ornamental plants may have greater success because they are likely to have been introduced in a suitable climate similar to that of their region of origin.

In many aspects, arable lands can be considered as very simplified ecosystems with few bottom-up and top-down regulations (Altieri 1999). The environment is strongly modified and controlled to optimize the growth of cultivated plants. Regular soil tillage, fertilisation, and irrigation lead to a high level of disturbances and soil resource availability. This situation also translates into a large amount of nutrient-rich biomass that makes the crop a very attractive resource for primary consumers, compared to the vegetation in the surrounding areas. Although arable fields constitute a mosaic of different crop species at the regional scale, the few dominant varieties used for each crop species result in a strong genetic uniformity over large areas. For example, in the USA, 60–70 % of the total common bean area is planted with only two or three varieties. Thus, management practices favour habitat characteristics that enhance biological invasions: low species richness, frequent disturbances, and high resource availability (Booth et al. 2003).

Considering both the extent and economic importance of biological invasions in crop fields, this chapter first reviews the patterns of invasion of non-native weeds, pests, and pathogens in arable lands with regard to pathways of introduction and biological traits, and then describes the causes and consequences of their impacts on crop production.

6.2 Patterns of Invasion in Arable Crops

6.2.1 Proportion of Non-native Species in Arable Crops

The inventories of non-native species available throughout the world show that arable lands often harbor the major part of non-native species established in a given area. In Europe, about 50 % of all non-native plants, and almost 30 % of all non-native arthropods, can be found in agricultural and horticultural lands (DAISIE 2009). In the USA, 73 %, 65 %, and 40 % of the weeds, pathogens, and insect pests of crops are non-native (Pimentel et al. 2005). These are very high proportions, considering that for the whole USA non-native insects and non-native plants constitute only 2 % and 18 % of the entire insect fauna or flora, respectively. The figures are lower for pathogens. In Europe, some 20 fungal pathogens of economic significance have been established since 1800 (Desprez-Loustau et al. 2010). In Great Britain, 30 species have been recorded on arable crops among the 235 species of plant pathogens of quite recent introduction (1970–2004) (Jones and Baker 2007).

6.2.2 Main Pathways and Biogeographical Origins

Most non-native weeds, pests, and pathogens have been introduced unintentionally as contaminants of agricultural or horticultural commodities, including seeds of crops for sowing (mostly for weeds), and other commodities, such as plants for planting or cut flowers (for pests and pathogens). These introductions started long ago, during the Neolithic Period (~6000 BC), with the spread from the Near East to Western Europe of weeds such as *Agrostemma githago* or *Cyanus segetum*, or insect fauna of stored grain such as the flightless weevil, *Sitophilus granarius*, or the beetle, *Tribolium confusum*.

There is often no agreement regarding the exact area of origin of weeds, pests, and pathogens, especially for “human commensal” species that achieved a cosmopolitan distribution long ago. It is often believed that their area of origin corresponds to the centre of origin of the crop with which they are associated. In Europe, the natural distribution range of many anciently introduced weed and pest species probably coincided with that of the wild progenitors of wheat and barley in the Near and Middle East and then travelled westwards with early agriculturists. Similarly, there is increased evidence on the emergence of pathogens within the crop diversification areas and their subsequent spread in association with crop domestication, human migrations, and the development of agriculture (Banke and McDonald 2005).

More recently, neophytic weeds (i.e., introduced after 1500 AD), such as species of *Amaranthus* or *Panicum*, were introduced in Europe from America with contaminated seeds of crops such as maize or soybean. In France, the second and the third most important area of origin of neophytic weeds is North America (20 %) and South America (16 %), just after the Mediterranean Basin (22 %). Similarly, a large proportion of the introductions of non-native weeds and insects in the USA were associated early with European migration and later by international trade with other continents. In Great Britain, the ten recently introduced plant pathogens of known origin were imported from the three countries of continental Europe (France, Netherlands, and Spain) with the largest crop production or export (Jones and Baker 2007). This scenario illustrates how the donor regions tend to reflect trends in the major trade flow of agricultural products.

6.2.3 General Biological Traits

Although it is difficult to find a common suite of traits shared by all or even most non-native invasive species in natural and seminatural habitats, the more homogeneous and stringent conditions prevailing in arable lands permits a broad picture of invasive species that succeed in such disturbed environments. They generally belong to the *r*-strategist species category, with traits such as high fecundity, short lifespan, high growth rate, and plasticity.

Based on the list of noxious weeds of the Weed Science Society of America, Kuester et al. (2014) showed that weedy plants (both native and non-native) are more likely to be annuals, exhibit a fast growth rate, and have high fruit abundance, high seedling vigour, and rapid vegetative spread. This list covers many traits of the ideal weeds defined by Baker (1965), but their relative importance for weed success can vary according to local cropping systems. Indeed, successful weeds can differ according to the crop types considered, based on the synchronisation of their life cycle (especially timing of emergence) with that of the crop or on their tolerance to the spectrum of herbicides used in the crop (Fried et al. 2009).

Certain traits predispose arthropods to establish successfully, such as their small size, good powers of flight, high rate of reproduction (many species are also parthenogenetic), ability to reach high numbers, cryptic behavior, egg deposition on or inside plant tissue or in soil, and propensity to secrete themselves in tight spaces (Roques et al. 2010). The likelihood of establishment also increases when the invader arrives with a large founding population and is preadapted to the new environment.

Pathogens, especially fungi, have a strong invasive potential because of their diversity of dispersal modes, their short generation time, and high fertility; most species exhibit phenotypic plasticity and evolutionary potential, which allows them to thrive in a wide range of environments (Desprez-Loustau et al. 2007).

6.3 Impact of Non-native Species on Crop Production

Decreases in crop production, or more specifically, yield losses, are calculated as the difference between the attainable and the actual yield (Fig. 6.1). Crop losses occur because the physiology of the growing crop is negatively affected by weeds, pests, and pathogens. Some non-native species have been involved in spectacular invasions that damaged crops over large areas in a few years and strongly affected human populations in the nineteenth century. The pathogen causing potato late blight, *Phytophthora infestans*, was one of the factors responsible for the Irish Potato Famine that caused more than 1 million persons to starve to death and forced another million to emigrate (Fig. 6.2). The struggle against the American vine phylloxera, *Daktulosphaira vitifoliae*, that destroyed most of the European vineyards in the late nineteenth century was the first example of international cooperation against a pest. This effort constituted the first steps that led to the creation of the IPPC (International Plant Protection Convention) that was established to facilitate international cooperation in controlling plant pests and to prevent their international spread (van der Graaff and Khoury 2010).

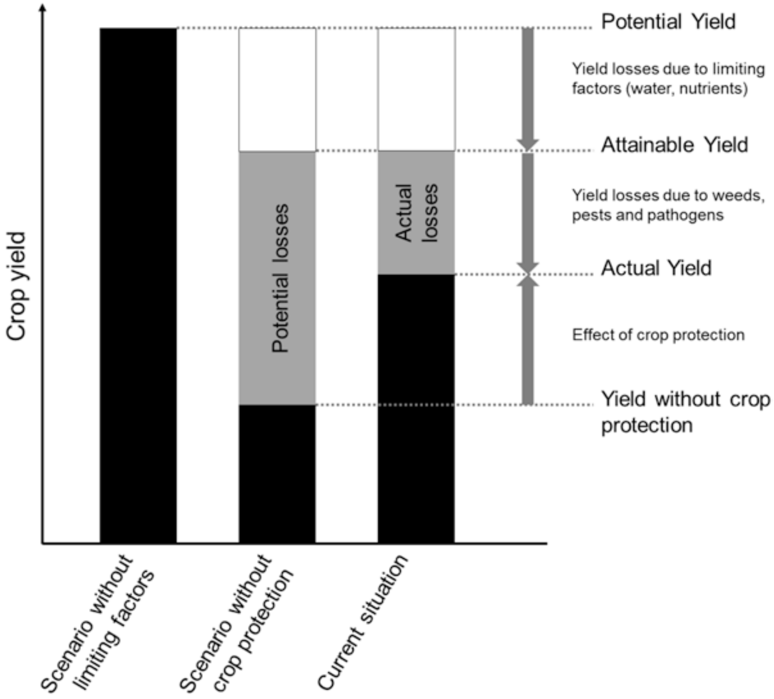

Fig. 6.1 The different yield levels and abiotic and biotic factors causing crop losses (From Oerke 2006 and other sources)

Fig. 6.2 Assessment of field resistance to potato late blight caused by *Phytophthora infestans*, in an array of potato cultivars left without fungicide protection. Resistant cultivars were hardly impacted by the disease while susceptible cultivars were totally defoliated (Photograph by D. Andrivon. © INRA Ploudaniel)

6.3.1 Mechanisms Underlying the Effects of Non-native Species on Crops

Damage mechanisms inducing crop losses can be classified into different categories based on the timing (i.e., before or after harvest of the crop), and on the direct and indirect nature of the effects on crop plants (see Table 6.1). Moreover, damages can result in a reduction of the quantity or the quality of the harvested crop.

6.3.1.1 Weeds

There are three primary mechanisms of interference between weeds and crops: competition, allelopathy, and parasitism. Most weeds have an effect on crop yield through resource competition for available light, water, and nutrients (Zimdahl 2004; Table 6.1). Another mechanism, which may have more impact in the case of newly introduced non-native weeds, is *allelopathy* (Table 6.2), that is, the release of chemical compounds that might have harmful effects on the growth of the crop

Table 6.1 Crop damage (or injury) mechanisms based on various sources

Timing of damages	Type of damages[a]	Damage mechanisms	Effect	Examples of harmful organisms
Pre-harvest	Direct	Stand (crop density) reducers	Weaken seeds or seedlings before or after they germinate; weaken the stem and cause the crop plant to fall over	Damping-off pathogens, arthropods, including Lepidoptera (cutworms), Coleoptera (rootworms) and Diptera
		Fruit/seed-feeders	Damage parts of plants that are harvested	Chewing and sucking arthropods, birds
	Indirect	Photosynthetic rate reducers	Reduce the rate of carbon uptake	Fungi, bacteria, viruses, gall making and leaf-mining arthropods
		Leaf senescence accelerators	Increase leaf senescence, causes defoliation	Pathogens, arthropods sucking cell contents and leaf-mining arthropods
		Tissue consumers	Reduce tissue biomass	Chewing arthropods, necrotrophic pathogens
		Turgor reducers	Disrupt xylem and phloem transport	Vascular, wilt pathogens, insects
		Assimilate sappers	Remove soluble assimilates from host	Nematodes, pathogens, phloem- or xylem-sucking arthropods, parasitic weeds
		Light stealers	Reduce the intercepted radiation	Non-parasitic weeds, leafspot pathogens
		Nutrient and water stealers (competition)	Reduce the nutrient & water uptake	Non-parasitic weeds
		Growth inhibitors/regulators	Prevent seedling emergence or regulates plant growth	Allelopathic weeds
Post-harvest	Direct	Fruit/seed-feeders	Reduce the number and biomass of marketable products	Stored grain arthropods, rodents, birds
	Indirect	Contamination of fruits or grains	Damage harvested organs	Fungi
		Market price downgrading	Decrease technological or visual quality	Fungi, bacteria, weeds, arthropods
		Food poisoning	Release toxins	Fungi, bacteria, poisonous weeds

[a] *Direct damages* refer to the injury of plant parts (e.g., destruction of yield forming, storage, and reproductive organs); *indirect damages* cover changes in plant architecture, reduced growth and development, quality losses or aesthetics, and transmission of diseases. Indirect impacts can also occur through competition, parasitism, or predation of beneficial organisms

Table 6.2 Average yield losses due to non-native weeds in different crops and regions

Non-native weed	Life form	Origin area	Introduced area	Mech.[a]	Crop	Weed density	Yield losses (% mean ± SD)[b]	Number of references[c]
Ambrosia artemisiifolia (Asteraceae)	Therophyte	N America	Europe	C	Sugarbeet	105/m^2	76 ± 8.5	2
			Europe	C	Potato	105/m^2	30[d]	1
			Europe	C	Maize	8–26/m^2	48.2 ± 16.4	4
			Europe	C, I	Sunflower	10–100/m^2	57.8 ± 30.8	4
Avena fatua (Poaceae)	Therophyte	Temp. Asia	N & S America, Europe	C, A	Cereals	70–660/m^2	43.3 ± 25.1	3
			N America	C	Legumes	32/m^2	44.6 ± 11.1	2
Chenopodium album (Amaranthaceae)	Therophyte	Europe	N America	C	Maize	5–110/m^2	26.8 ± 11.2	3
			N America	C	Soybean	9–16/10 m^2	22.8 ± 7.6	2
Cirsium arvense (Asteraceae)	Geophyte	Europe	N America	C, I	Cereals	14–30/m^2	45.0 ± 12.7	3
			N America	C	Alfalfa	10–20/m^2	41[d]	1
Cynodon dactylon (Poaceae)	Geophyte	Trop. Africa	N America, Europe	C, A	Spring crops	200–400 stems/m^2	58.0 ± 18.2	1
Cyperus rotundus (Cyperaceae)	Geophyte	Trop. Asia and Africa	N & S America	C	Vegetable crops	75–125/m^2	58 ± 23.4	5
				C	Rice	–	50[d]	1
Echinochloa crus-galli (Poaceae)	Therophyte	Trop. Asia	N America	C	Spring crops and legumes	1–5/m^2	58.7 ± 36.7	3
Lolium rigidum (Poaceae)	Therophyte	Europe	C America	C	Winter crops	300/m^2	31.8 ± 7.5	1
			Australia					

Parthenium hysterophorus (Asteraceae)	Therophyte	C America	Trop. Asia	C, A, I	Various crops	–	26.7 ± 12.6	3
Phelipanche ramosa[e] (Orobanchaceae)	Therophyte	Europe	C & S America	P	Legumes	–	50[d]	1
			S America	P	Tobacco			
Solanum elaeagnifolium (Solanaceae)	Geophyte	N America	N Africa, Australia	C, I	Various crops	5–6/m^2	46.4 ± 20.2	2
Sorghum halepense (Poaceae)	Geophyte	Temp. Asia	Europe, N America	C; A	Cotton	16–200 stems/m^2	71.2 ± 10.2	2
			Europe	C	Maize	100–200 stems/m^2	78.7 ± 25.8	3
			N & S America	C	Sugarcane	–	48.1 ± 23.3	2
			N America	C	Soybean	–	73.5 ± 20.5	1

[a] *C* competition, *A* allelopathy, *P* parasitism, *I* indirect effects

[b] Yield losses correspond to potential losses (see Fig. 6.1) based on experimental studies comparing weed-free field plots and plots with different quantities of weeds

[c] Indication of the number of studies on which the values are based

[d] The figures give the number of references on which the mean crop yield losses has been computed

[e] In most cases parasitic weeds are harmful to crops in their native range in the drier and warmer areas of Africa and Asia (*Striga*) and in the Mediterranean Basin (*Orobanche*, *Phelipanche*). A few species have been recorded outside their native range, for example, some species of *Cuscuta*, *Striga asiatica* in the USA, or *Phelipanche ramosa* in Australia and in America

(Willis 2007). Although allelochemical properties of weed residues are often short lived, their effects could be sufficient to favour the establishment of the weeds in the field at the expense of the crop. Allelopathy seems to be a main factor in the success of some non-native weeds, such as *Centaurea diffusa* in forage crops (e.g., *Pseudoroegneria spicata* or *Festuca scabrella*) in North America, or *Parthenium hysterophorus* in annual cereals (corn and sorghum) in Asia and Africa. Some parasitic weeds, such as witch weeds (*Striga* spp.), broomrapes (*Orobanche* spp. and *Phelipanche* spp.), or dodders (*Cuscuta* spp.), affect crop plants directly by connecting their haustorium to obtain water with its nutrients in the sap. Their derivation of nutritional requirements induces a short- or medium-term weakening of the annual crops, often continuing until harvest or leading to the death of the cultivated species (Parker 2009). The mechanisms that could explain the particular effects of non-native parasitic weeds on a new host crop encountered in the area of introduction are similar to those for crop pathogens (see Sect. 6.3.1.3).

6.3.1.2 Pests

The great diversity of arthropods feeding on plants demonstrate a remarkable diversity of lifestyles, mouthparts, and gut morphological adaptations to the food eaten. In relationship to the range of plant taxa used, monophagous insects feed on one plant taxon, oligophagous insects feed on few, and polyphagous insects are generalists that feed on many plant groups. Non-native arthropods injure plants directly through feeding or, indirectly through the transmission of plant pathogens. Feeding on green plants (phytophagy) causes plant tissue damages that are prejudicial for plant growth, survival, or reproduction of a variety of agricultural crops. Non-native arthropods include species that attack roots, stems, leaves, flowers, and fruits, either as larvae or as adults or in both stages. Leaf feeders may be external or they may mine tissues. There are many different ways that arthropod pests cause losses in plant yield by feeding directly on cultivated plants (see also Table 6.1).

- Leaf-chewing arthropods dominated by Lepidoptera, Coleoptera, or some myriapods, which can occasion severe defoliation, stem or root boring, and feeding on flower or seed structures
- Sucking arthropods, such as Hemiptera, Thysanoptera, or Acari, which drain plant resources by removing phloem or xylem contents or by sucking cell contents, leading to tissue necrosis, distortion, or stunting of shoots
- Leaf-mining species, mainly larvae of Hymenoptera, Lepidoptera, and Diptera, which cause leaf damage that appears as tunnels, blotches, or blisters
- Gall-making species (Diptera, Hymenoptera, Thysanoptera, and Acari), which alter, often substantially and characteristically, the morphology of plant parts

Many pests transmit economically important pathogens from infected to healthy hosts. Transmission of phytopathogenic viruses and bacteria by aphids, thrips, whiteflies, leafhoppers, planthoppers, treehoppers, fruit fly, flea beetles, psyllids, mites, and nematodes is well known.

6.3.1.3 Pathogens

A plant disease results from a compatible interaction that occurs as a result of a pathogen being able to overcome the resistance mechanisms of the host plant. Plant and pathogens sharing the same distribution area for long time periods have developed co-evolutionary mechanisms, often termed an arms race. Host resistance triggers an increase or a shift in pathogen virulence, which in turn enhances increased host resistance, and so on. This kind of plant–pathogen interaction was termed ‘old encounter’ by Robinson (1976). In crops, the co-evolutionary process includes breeding programs that involve selection for resistance to the main pathogens.

Introduction of a non-native pathogen in a given area results in a ‘new encounter’. Plant populations that have never encountered the pathogen, and therefore probably do not have resistance to it, are especially vulnerable to the newcomer, even more so when grown on large areas with limited genetic diversity, as is the case in most modern agro-ecosystems. In several cases, the new encounter is indeed a re-encounter: plants have been transported, pathogen free, to a new continent, where they have evolved or have been bred without pathogen pressure, therefore losing any original resistance factor. The introduction of the pathogen decades or centuries after the introduction of the plant can make the re-encounter fatal to the plant.

The most emblematic case of such a re-encounter is the inadvertent introduction of the oomycete causing potato late blight in Europe in the 1840s, more than three centuries after the introduction of the potato in Europe. Other significant examples are the introduction of chrysantheme rust, *Puccinia horiana*, in Europe (1900s); coffee rust, *Puccinia horiana*, and sugarcane rust, *P. melanocephala*, in the Americas; wheat stripe rust, *P. striiformis*, in Australia (1979); and of soybean rust, *Phakopsora pachyrhizi*, in the USA (2004). Such re-encounters can be expected to happen at some point when pathogens have the capacity for long-distance dispersal, via either wind or human transportation.

6.3.2 Negative Consequences on Crop Production

The relationship between weed or pest density or disease intensity and crop damage is critically dependent of the identity of the species and cultivars involved, as well as the cropping system and environmental conditions, with strong variation among years (Oerke 2006). Moreover, many reports of crop losses rarely differentiate the part caused by non-native species only. However, based on a few review articles that estimate average yield losses attributable to harmful organisms for the main crop species worldwide (Oerke 2006), and according to the relative proportion of native and non-native weeds, pests, and pathogens in different areas, a crude estimate of the impacts of non-native harmful organisms is possible.

The average potential losses (i.e., without crop protection) (see Fig. 6.1) are typically higher for weeds (23–43.6 % of attainable yield) than for animal pests (8.7–36.8 %) or for pathogens (8.5–21.2 %). However, because of higher efficacy of weed control, actual losses are almost similar among the three taxa: 7.5–10.5 %, 7.9–15.1 %, and 7.2–14.5 % for weeds, pests, and pathogens, respectively (Oerke 2006). In US agriculture, the loss from non-native weeds, pests, and pathogens was estimated to be $26.92, $14.4, and $21.5 US billion/year, respectively (Pimentel et al. 2005) (Fig. 6.3). In Western Europe, for example, in the UK, the production per hectare is greater than in North America, resulting in higher control costs relative to direct crop losses and higher impact of non-native pathogens compared to the other taxa (Fig. 6.3).

6.3.2.1 Weeds

It is difficult to simply categorise non-native weed species according to their impacts. The direction and magnitude of the effects of weed–crop competition for resources are related to their density and to environmental conditions, especially soil moisture or nutrients (Zimdahl 2004). The impact of a given weed also depends on the identity of the invaded crops, the duration of the interference, and the life history stage of the weed–crop system at which the interaction takes place (Vilà et al. 2004). Three traits are particularly relevant to the magnitude of the effect of competition on the crop.

- *Time of weed emergence compared to the crop species*: this is related to the duration of weed-free conditions. The effects of competition for resources are expected to be more important between taxonomically close species (e.g., *Ambrosia artemisiifolia* on sunflower; *Panicum* spp. on maize). In addition, taxonomic proximity makes selective weeding control methods (chemical and mechanical, seed sorting) more difficult. For example, large infestations of *A. artemisiifolia* can induce a complete destruction of sunflower fields (Table 6.2). In the EU, the economic cost of *A. artemisiifolia* through the loss of agricultural production has been estimated to €1846 million/year.
- *Growth rate*: weeds that are able to grow tall, reach high cover, or achieve rapid lateral spread will gain a competitive advantage, which is why perennial weeds such as *Cirsium arvense* or *Sorghum halepense* are so harmful in cereal crops. The reserves stored in their underground organs make them able to grow faster and more vigorously than the annual crops and ensure survival and escape from chemical treatments and superficial tillage. For example, 10–30 shoots/m^2 of *C. arvense* are sufficient to cause more than 40 % yield losses, with crop loss exceeding 70 % in dense patches (Tiley 2010).
- *Weed size relative to that of the crop*: differences in size between weed and crop species are thought to be a robust predictor of yield losses. This is one of the factors that make *Avena fatua* (that reaches up to 150 cm height) one of the most important and competitive grass weeds of winter and spring cereals (~85 cm height on average), resulting in 5 % yield loss from as few as 5 plants/m^2 (Beckie et al. 2012). In the prairie provinces of Canada, annual losses from *Avena fatua* vary from CAN$120 million up to CAN$500 million (Beckie et al. 2012).

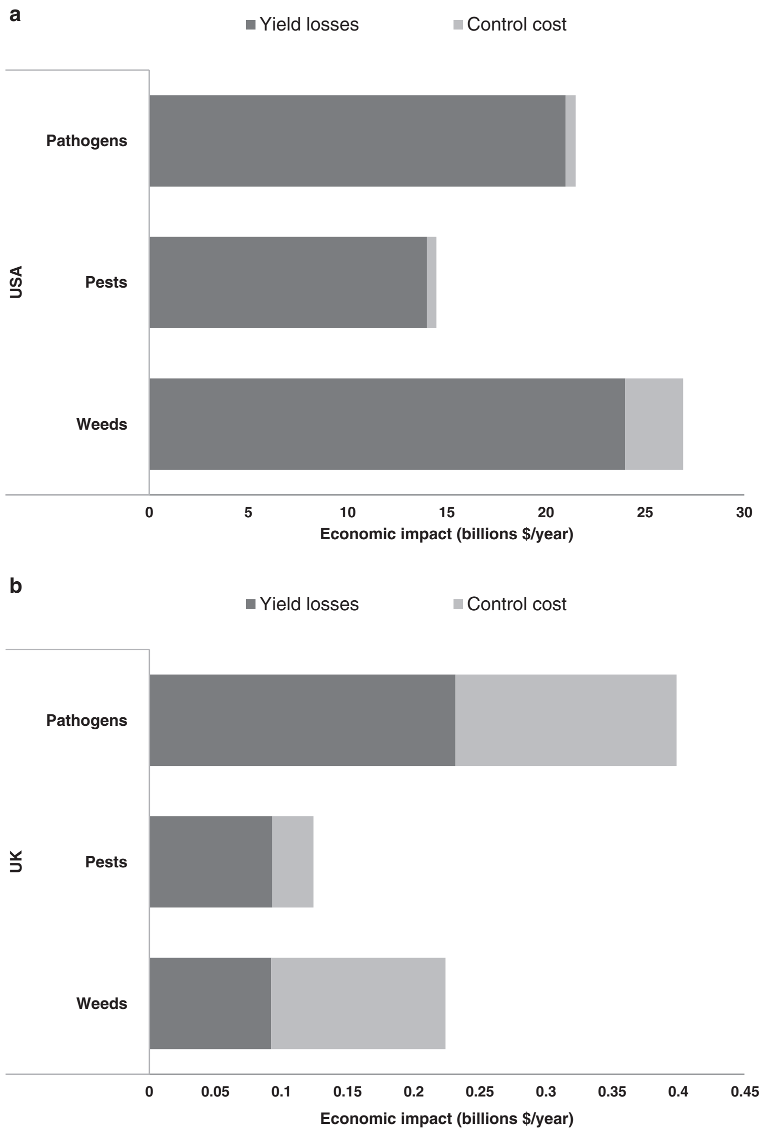

Fig. 6.3 Economic impacts of non-native weeds, pests, and pathogens on crops (billions $/year) in (**a**) the USA (data from Pimentel at al. 2005) and (**b**) the UK (Data from Williams et al. 2010)

Globally, parasitic weeds are not common; threatened crops represent about 4–5 % of the world's arable land. However, where present, these weeds can be very impressive in their effects. In the USA, it was estimated that the spread of *Striga asiatica* following its introduction in 1956 would have led to weed control costs of US$1 billion per year, beside total losses of yield of at least 10 % each year. Across four decades, the cost of eradication of *S. asiatica* has totalled US$250 million.

Fig. 6.4 Strong density of common ragweed, *Ambrosia artemisiifolia*, in a weeded sunflower field (France, August 2015) (Photograph by R. Bilon © Observatoire des ambroisies)

Although several weeds impact crop yield through both competition and allelopathy (Table 6.2), the latter mechanism is considered the primary one in only a few species; for example, crop losses of up to 40 % reported for *Parthenium hysterophorus* in Asia and Africa occur primarily through allelopathic effects.

Finally, invasive non-native weeds can also have indirect effects on the quality of farm products or even on the whole cropping system. Even at low density, seeds or leaves in harvested products (grain or forage) can cause a decrease in quality or problems of human or livestock poisoning (e.g., *Datura stramonium*). The efficiency of control of *Ambrosia artemisiifolia* is sometimes so poor that farmers avoid introducing sunflower in their rotation when ragweed seed density is too high (Fig. 6.4). In the early days of settlement in North America, the difficulty in controlling *Cirsium arvense* was such that it often led to the abandonment of whole farms (Tiley 2010). In Morocco, agricultural land infested with *Solanum elaeagnifolium* results in a decrease by 25 % in the rental and resale of infested fields.

6.3.2.2 Pests

The combination of the numbers of the pest present, their development stage, and the duration of the pest attack on the crop influences the intensity of crop losses. Full costs of most potential invasive arthropods are still poorly known, and most risk

Fig. 6.5 Adult of brown marmorated stink bug, *Halyomorpha halys*, feeding on an apple. *Halyomorpha halys* attacks tree fruit, small fruit, vegetables, and ornamentals. In tree fruit, economic damage has resulted in increased production inputs and secondary pest outbreaks in affected countries (Photograph by J.-C. Streito © INRA Montpellier)

assessment studies rely on expert judgment or rudimentary analytical approaches. A few well-known examples are described here.

One of the first major non-native pests to affect the European economy was the American vine phylloxera, *Daktulosphaira vitifoliae*. In the late nineteenth century, this small sap-sucking insect completely destroyed nearly one-third of the French vineyards, that is, more than 1,000,000 ha, with incalculable economic and social consequences. At the beginning of the twentieth century, the introduction of the boll weevil, *Anthonomus grandis*, from Mexico to North America resulted in billions of dollars of damage and the almost complete eradication of the cotton crop in the USA. The most widespread insect pest throughout the US corn belt has been the European corn borer, *Ostrinia nubilalis.* This pyralid moth was accidentally introduced into eastern USA in 1917 and subsequently spread with devastating results. Losses are estimated to be US$1 billion per year (Hutchison et al. 2010). The pest is now controlled through reductions in its populations resulting from genetically engineered Bt maize.

Any continent is now facing major challenges from increasing non-native arthropods attacking crops. The brown marmorated stink bug, *Halyomorpha halys*, is a polyphagous sucking insect native to Asia that invaded the USA in the mid-1990s. In 2010, it resulted in up to US$37 million losses for apple alone in the mid-Atlantic region (Fig. 6.5). Some stone fruit growers lost 90 % of their crop (Leskey et al.

2012). The rice water weevil, *Lissorhoptrus oryzophilus*, was accidentally introduced from North America into Japan on infested rice straw in 1976, with subsequent yield losses of 41–60 % caused by root pruning and chlorosis of seedlings. *Drosophila suzukii* is thought to be a native of eastern and southeastern Asia. It was first detected in mainland USA in 2008 and simultaneously in Europe. The larval stage of this small drosophilid infests and develops in undamaged ripening fruits, rendering the fruit unmarketable. Preliminary studies in the USA (Bolda et al. 2010) indicate an annual loss of more than US$500 million in five affected crops (strawberries, blueberries, raspberries, blackberries, cherries) in three states (California, Oregon, and Washington). In France, yield loss estimates from 2013 observations range from negligible to 100 % on cherry crops.

6.3.2.3 Pathogens

Several plant pathogens directly decrease yield by killing crop plants (blights, rots) or decreasing biomass production (rusts, powdery mildews), but not killing the plants. Because of their explosive spatiotemporal dynamics and environmental plasticity, pathogens can annihilate yield in plots not protected by either genetic resistance or pesticide sprays. The Asian soybean rust, introduced in the Americas in 2001, claimed 5 % of the annual production in Brazil; in the USA, the annual net economic losses were anticipated to range from US$240 million to US$2 billion, depending on the severity and extent of subsequent outbreaks (Fig. 6.6). Increased early warning, monitoring, and education, however, resulted in the control of the disease, saving farmers more than US$200 million annually in unnecessary fungicide applications (Sikora et al. 2014). In Switzerland, the control of fire blight, a quarantine invasive disease of Maloideae caused by the bacterium *Erwinia amylovora*, has cost 29 million Swiss francs over a 10-year period.

Plant pathogens with less direct or even no significant effect on yield can also decrease production by making the crop plants unsuitable for marketing. Vegetables, fruit, and flowers with disease symptoms (spots, chlorosis) lose commercial value and are banned from use in industrial processing. Potatoes with malformation induced by the Potato spindle tuber viroid will no longer fit the processing standards and will be discarded. The generalised spread of the disease to Europe, where it now occurs only sporadically, would cause an annual loss for the producers of €567 million and require control measures costing €118 million (Soliman et al. 2012). Finally, some pathogens produce secondary metabolites that represent a risk for cattle and human health. Ergotism is an historical issue that is currently re-emerging, and the production of carcinogenic toxins by several species of *Fusarium* infecting wheat is the subject of norms and regulations all over the world.

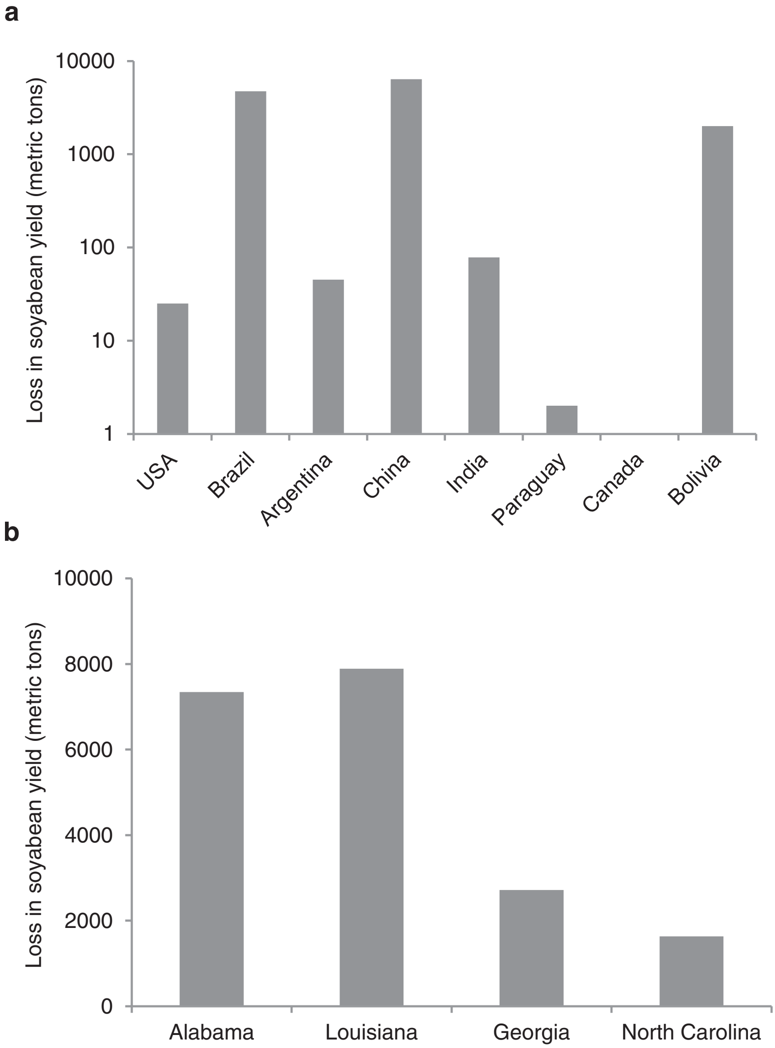

Fig. 6.6 Estimated reduction of soybean yields caused by soybean rust in 2006 in (**a**) the world's top eight soybean-producing countries (thousand metric tons; note the logarithmic vertical scale) and (**b**) the USA top four soybean-producing states (metric tons; note the linear vertical scale) (Data from Wrather et al. 2010)

6.4 Conclusions

Several economic assessments have stressed that agriculture is the sector being most affected by the introduction of non-native species. Introduced weeds, pests, and pathogens cause annual losses to world agriculture estimated between US$55 billion and US$248 billion (Pimentel et al. 2001). Of the US$120 billion/year of damages associated with non-native species in the USA, US$62.2 billion/year (52 %) are caused by species invading crops (Pimentel et al. 2005). In UK, 64 % of the £1.67 billion/year economic impact of non-native species concerns agriculture (Williams et al. 2010). Pesticide application has traditionally been an effective and economical means of reducing crop losses and ensuring that new species do not proliferate in arable land. However, overdependence on pesticides has negative impacts on the environment and has dramatically favoured the development of resistant biotypes. To reduce crop losses and arable land vulnerability to invasions, a more sustainable, integrated, and holistic approach is needed (Harker et al. 2005): this should include higher prevention measures at the international level (i.e., pathways risk assessment, surveillance, early detection, and rapid eradication) and restore, as much as possible, ecological regulation (competition, predation, parasitism) at the landscape and field level. This integrated approach will also require ensuring optimal crop canopy health, selecting competitive and resistant cultivars, optimising seeding density and careful seed placement, strategic fertilisation and watering, but also more diverse crop rotations.

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Chapter 7
Impact of Non-native Invertebrates and Pathogens on Market Forest Tree Resources

Marc Kenis, Alain Roques, Alberto Santini, and Andrew M. Liebhold

Abstract Several forest non-native pests and pathogens that are among the most frequently cited invasive species worldwide represent serious economic and conservation concerns for the forest ecosystems in their region of introduction. Such organisms can have adverse impacts on the yield of marketable wood products, such as timber and pulp, as well as non-wood forest products, such as nuts, fruits, and seeds. However, quantitative data about impacts on forest market resources are rare and usually restricted in time and space. Moreover, information on regional impacts, and aggregate data including multiple invasive species, are largely missing or miscalculated. The most comprehensive studies show that the greatest impacts of pest invasions on native tree species are effects on non-market values whereas losses in wood and non-wood forest products account for a small part of the total impacts. Patterns are somewhat different in plantations of non-native trees, where non-native pests are more likely to affect the forestry sector directly through reduced fibre yield and increased management costs, whereas non-market values and environmental impacts are of lesser concern. This chapter argues that direct impacts on market forest resources are sometimes largely exaggerated and provides reasons for these overestimations.

Keywords Economic impact • Forestry • Forest market resources • Invasive pests • Non-native trees • Non-wood forest products • Yield loss

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7.1 Introduction

Non-native damaging invertebrates and pathogens (hereafter pests) are a critical and increasing threat to trees and forest ecosystems. In contrast to many other invasive species arriving on new continents intentionally, tree pests are nearly always introduced accidentally, usually through the trade in live plants, wood, or wood products (Liebhold 2012). As a result, their introduction is particularly difficult to control and, despite the intensification of phytosanitary measures worldwide, the number of new establishments of non-native tree pests and their damage continue to increase (Aukema et al. 2010).

Although most non-native pests cause little impact, a few species cause substantial damage to their host trees and, in a few cases, can locally eliminate tree species and alter ecosystems (Kenis et al. 2009). Native forests of eastern North America have suffered particularly from non-native pests in the past century, with the strong decline of keystone species such as the American chestnut (through chestnut blight, *Cryphonectria parasitica*), elms (Dutch elm disease, *Ophiostoma ulmi* and O. *novo-ulmi*) (Fig. 7.1), eastern and Carolina hemlock (hemlock woolly adelgid, *Adelges tsugae*), Fraser fir and other firs (balsam wooly adelgid, *Adelges piceae*), and ash species (emerald ash borer, *Agrilus planipennis*) (Aukema et al 2010; Liebhold et al. 2013). Such declines affect ecosystems and their services in many ways.

Fig. 7.1 Elm tree killed by Dutch elm disease, *Ophiostoma ulmi* and *O. novo-ulmi*, in Italy (Photograph by Alberto Santini)

This review is restricted to the impact on production of marketable tree resources, that is, provisioning ecosystem services. For most forests, the primary market product is wood fibre, utilised primarily for lumber, pulp, and fuel, but non-wood forest products (NWFP) such as nuts, fruits, and seeds are also considered. The important ecological impacts that these invasive species have in forests on supporting, regulating, and cultural ecosystems services and human well-being are not considered, although it is clear that all these services are closely interconnected. Effects on ornamental trees and the ornamental plant market are also excluded.

Some studies indicate that wood and NWFP losses account for a small part of the economic impacts of forest pests, the largest part being represented by non-market tree values, such as loss of property values or federal and local government expenditures (Holmes et al. 2009; Aukema et al. 2011). They account for an even smaller part of the impacts when all ecosystem services are considered, even if comparing ecosystem services remains a challenge (Branco et al. 2015). This problem is particularly acute when pests affect native keystone tree species (Kenis et al. 2009; Aukema et al. 2010).

7.2 Impact on Wood Fibre Production

Impacts on wood fibre production can involve at least three mechanisms: first, pests can affect tree growth increment; second, they can kill mature trees; and third, they can affect regeneration by killing seeds or seedlings in either a seed orchard or nursery or a forest stand. Obviously, the same pest can affect wood production in two or three ways. Another useful categorisation is whether the pest affects native trees or plantations of non-native trees. This concern is important because damage to non-native plantations is likely to affect primarily the forest industry through wood fibre losses and management costs related to invasion, such as mandatory fumigations, whereas pests affecting predominantly native trees are likely to have more complex and integrated economic, social, and ecological impacts in which the damage to the forestry sector may be marginal. However, it is remarkable how few quantitative studies on their impact on wood production have been published. Most data only concern a single species in a single country or even in a specific stand during a limited period of time. Information on regional impacts and aggregate data including multiple pest species are largely missing. Table 7.1 provides a nonexhaustive list of forest pests for which some type of quantitative assessment of their damage to wood and non-wood forest products has been estimated.

7.2.1 *Damage to Native Tree Species*

One of the most comprehensive studies on the economic impact of forest pests was that of Aukema et al. (2011), who calculated the economic damage caused by three pests affecting mainly native trees in the USA: *Agrilus planipennis*, *Adelgid tsugae*,

Table 7.1 Examples of quantitative data of effects of forestry pests and pathogens on wood production (native and non-native trees) and non-wood forest products

Trees and country	Invasive species	Damage	References
Wood: native trees			
Hemlock in USA	*Adelges tsugae*	Average of US$ 1.1 million/year in timber loss (0.5 % of total costs)	Aukema et al. (2011)
Ash in USA	*Agrilus planipennis*	Average of US$ 60 million/year in timber loss (3.6 % of total costs)	Aukema et al. (2011)
Ash in Essex County, Canada	*Agrilus planipennis*	CAN$ 14–16 million/year for control	Colautti et al. (2006)
Pines in Japan	*Bursaphelenchus xylophilus*	Wood losses exceed 2,000,000 m^3 per year	CABI (2015) and references therein
Chestnut in eastern USA	*Cryphonectria parasitica*	Almost all canopy or 3.5 billion American chestnut trees were killed	CABI (2015) and references therein
Broadleaved trees in USA	*Lymantria dispar*	Average of US$ 4.6 million/year in timber loss (1.8 % of total cost)	Aukema et al. (2011)
Broadleaved trees in New England, USA	*Lymantria dispar*	Up to 50 % reduction in annual growth increment	Muzika and Liebhold (1999)
Broadleaved trees in Québec, Canada	*Lymantria dispar*	Average of 44 % reduction in annual growth increment in host trees	Naidoo and Lechowicz (2001)
Oak in Massachusetts, USA	*Operophtera brumata*	Up to 47 % reduction in annual radial growth	Simmons et al. (2014)
Elms in Europe and North America	*Ophiostoma ulmi* and *O. novo-ulmi*	Hundreds of millions of elms killed by the two Dutch elm disease pandemics	CABI (2015) and references therein
All forests in USA (mostly native)	Many invertebrates and pathogens	US$ 4.2 billion/year	Pimentel et al. (2000)
Canadian forests (mostly native)	Seven pests (projections)	CAN$ 9.6 billion ($7.7 billion to $20 billion)	Colautti et al. (2006)
Wood: non-native trees			
Pinus radiata in New Zealand	*Armillaria novae-zelandiae*	Reduction of 14–24 % in growth increment of 8- to 10-year-old trees	Shaw and Taes (1977)
Cypress in East Africa	*Cinara cupressivora*	Up to 1990, killed trees worth US$44 million and was causing an additional loss of a further US$14.6 million per year through reduction in annual growth increment.	Cock (2003)

(continued)

Table 7.1 (continued)

Trees and country	Invasive species	Damage	References
Pinus radiata in New Zealand	*Dothistroma septospora*	Annual cost to the forestry industry in New Zealand was estimated to be NZ$6.1 million in the 1980s in terms of direct control costs and residual growth loss	CABI (2015) and references therein
Pinus radiata in New Zealand	*Dothistroma septospora*	Reduction of 17–73 % in growth increment of 8- to 10-year-old trees	Shaw and Taes (1977)
Spruce in UK and Northern Europe	*Elatobium abietinum*	Reduces height increment by 20–60 % in the year of attack; reduces diameter increment for 7–8 years, with a mean reduction of 18.5–40.5 %.	CABI (2015) and references therein
Eucalyptus in Spain	*Gonipterus platensis*	Estimated to reduce tree growth by 30 %, causing an economic loss of $10.5 million annually in Galicia	Branco et al. (2015) and references therein
Eucalyptus in Portugal	*Gonipterus platensis*	Wood volume was estimated to decrease to 51 % in the affected areas in 2004–2006, with losses increasing exponentially with tree defoliation, by up to 43 % and 86 % corresponding to 75 % and 100 % defoliation, respectively.	Branco et al. (2015) and references therein
Eucalyptus in Spain	*Phoracanta semipunctata*	Loss of US$ 9 and 7 million for an area of 300,000 ha in Spain in 1983 and 1984	Branco et al. (2015) and references therein
Pines in East Africa	*Pineus boerneri* and *Eulachnus rileyi*	Loss of US$2.4 million per year caused by reductions in annual growth increment.	Cock (2003)
Pinus radiata in New Zealand	*Sirex noctilio*	Mortality rates of 30 % in 1946–1951	CABI (2015) and references therein
Pines in Australia	*Sirex noctilio*	Mortality rates of 40 % in Tasmania and up to 75 % in Victoria between 1932 and 1979; death of 5 million trees with a value of AUS $10–12 million in Southern Australia between 1987 and 1989	CABI (2015) and references therein

(continued)

Table 7.1 (continued)

Trees and country	Invasive species	Damage	References
Pines in Brazil	*Sirex noctilio*	Mortality rate of 60 % in Brazil in 1989.	CABI (2015)
All forests in UK (mostly non-native)	Many invertebrates and pathogens	US$ 2 million/year	Pimentel et al. (2000)
Non-wood forest products			
Chestnut in USA	*Cryphonectria parasitica*	Almost all mature chestnut trees killed in USA	CABI (2015) and references therein
Chestnut in Italy	*Dryocosmus kuriphilus*	Up to 80 % losses in chestnut production	Battisti et al. (2014)
Edible pine nuts in Italy	*Leptoglossus occidentalis*	Of the 2-year-old conelets, 80 % damaged	Roversi et al. (2011)
Conifer orchards in France	*Leptoglossus occidentalis*	Up to 25.7 % of the potential seed yield in Douglas-fir plantations in 2010, and by more than 15 % these of *Pinus nigra* and *P. sylvestris* in 2011	Lesieur et al. (2014)
Douglas-fir seed orchards in France	*Megastigmus spermotrophus*	Up to 95 % of loss of commercial seed crop	Auger-Rozenberg and Roques (2012)

and the gypsy moth, *Lymantria dispar*. They classified economic losses in five categories: (1) federal government expenditures (survey, research, regulation, management, and outreach); (2) local government expenditures (tree removal, replacement, and treatment); (3) household expenditures (tree removal, replacement, and treatment); (4) residential property value losses; and (5) timber value losses to forest landowners. For the three species, average annual timber losses in 2009 were estimated at US$60 million, US$1.1 million, and US$4.6 million, respectively. Interestingly, this represented only 3.6 %, 0.5 %, and 1.8 % of the total estimated costs calculated for the three insects, the majority of the costs affecting non-market values and borne by homeowners and municipal governments. When extrapolated across all non-native forest insect pests of the three main guilds (phloem and wood borers, sap feeders, and foliage feeders), the total annual cost was nearly US$5 billion, of which only US$65.7 million was related to timber value loss.

Interestingly, in an earlier study, Pimentel et al. (2000) had estimated the annual losses of timber caused by non-native pests to be much higher, that is, US$4.2 billion (arthropods and pathogens accounting for 50 % each). This estimate was based on an assumption that all (native and non-native) forest pests reduce overall timber productivity by 18 % and non-native species account for 30 % of the damage caused by all forest pests. Colautti et al. (2006) presented several cases of the economic costs of invasive species, including control costs for *O. ulmi* and *O. novo-ulmi* in Manitoba and of *A. planipennis* in a specific county. They also projected the economic losses in value to forest products in Canada to be CAN$9.6 billion (ranging from CAN$7.7 billion to CAN$20 billion). Although these and other basic calculations of economic impacts of invasive species have been useful for drawing attention to the significance of pests, they have been criticised for various reasons, such as failing to account for nonmarket economic values and the ability to substitute one resource for another and double-counting certain costs (Holmes et al. 2009; Aukema et al. 2011). Estimates in Colautti et al. (2006) were made using a price-times-quantity method (Holmes et al. 2009) in which impact is estimated as simply the volume of trees killed multiplied by a stumpage price. This method is problematic because it fails to account for the fact that (1) many affected stands would never be harvested; (2) other stands will be harvested sometime in the future and during this lag surviving trees will grow and compensate for the damage; and (3) forest managers may salvage affected trees, thereby recouping partial losses, or they may adjust their business plan in other ways (e.g., delay harvest or substitute other products). Unfortunately, the price-times-quantity method has been applied in other impact estimates as well.

Although historically European forests have suffered less from non-native pests than other continents, new forest pests are now introduced at a faster rate in Europe than in other continents. A long list of newly established species is threatening European forestry and urban forestry (Roques 2010; Santini et al. 2013). As elsewhere, economic impacts of pests on native ornamental trees are greater than in natural forests and, consequently, costs are mainly borne by municipalities and private owners. For example, damage by *O. ulmi* and *O. novo-ulmi* has cost €9–228 million annually since 1979, but mainly for felling and replacing ornamental trees in urban areas (Gren et al. 2009). High costs are also related to control measures, in particular mandatory phytosanitary measures related to eradication or containment programmes. The large efforts to eradicate and contain the pine wood nematode *Bursaphelenchus xylophilus*, causal agent of the pine wilt disease in Portugal, has been described in detail by Sousa et al. (2011). Although recent estimations of the costs to the Portuguese and EU authorities and the private sector are not available, they are undoubtedly much higher than the loss of timber directly attributable to the pest. Nevertheless, they are surely justified because damage at the European scale could be substantial. Soliman et al. (2012) estimated that an unregulated infestation of *B. xylophilus* in the EU could cause a loss of forestry stock over 22 years (2008–2030) that would cost €22 billion. In Japan, where the nematode is also invasive, wood losses exceed 2,000,000 m^3 per year (CABI 2015). Other examples of pests for which management costs for eradication or containment have so far largely exceeded direct wood losses are the two Asian longhorned beetles, *Anoplophora glabripennis* and *A. chinensis*. In the past two decades, both species have been under costly eradication programmes in various regions in Europe and North America. For example, from 1997 to 2006, US federal, state, and local authorities have spent more than US$800 million on *A. glabripennis* eradication measures in urban settings, involving surveys, removal, treatment to destroy all life stages present (e.g., chipping), and replacement (Smith and Wu 2008).

An example of a pathogen threatening native wood fibre production is the fungus *Cronartium ribicola*, the agent of the white pine blister rust. This pathogen

Fig. 7.2 Defoliation by gypsy moth, *Lymantria dispar*, in the United States (Photograph by Tim Tigner, Virginia Department of Forestry, Bugwood.org)

completes its life cycle between five-needle pines (*Pinus*, subgenus *Strobus*) and plants of the genus *Ribes*. This fungus is able to kill trees of all ages, but the rust is particularly damaging in young stands, preventing them from growing to a merchantable age. *Cronartium ribicola* is considered endemic to Siberia and was first reported in eastern North America in 1906 and western North America in 1921. It has become the most important disease of several white pine species in North America (Maloy 1997). However, damage is now most severe in Western North America, for example, on *Pinus monticola, P. flexilis*, *P. albicaulis*, and *P. lambertiana*, for which mortality rates of 95 % have been reported in Sierra Nevada. These species are not extensively planted for timber, and thus the pathogen now causes more concern for its environmental impact than for its impact on the forest industry (CABI 2015).

In contrast to bark and wood borers and certain tree pathogens, defoliators and sap feeders often do not directly kill trees but more commonly affect wood fibre production through growth losses. Outbreaks of the gypsy moth in North America can cause up to 50 % reduction in annual growth increment in broad-leaved trees (Muzika and Liebhold 1999; Naidoo and Lechowicz 2001) (Fig. 7.2). Simmons et al. (2014) also reported a growth rate reduction of nearly 50 % as a result of defoliation of oak by the winter moth, *Operophtera brumata*. However, defoliation can often lead to crown dieback and ultimately tree mortality, although very often secondary insects and pathogens are involved. In the case of outbreaks of the invasive gypsy moth in North America, this mortality can sometimes be extensive, especially in oaks, but then increased growth typically occurs in non-hosts and surviving hosts consequent to a thinning effect. As such, in many areas with a long history of gypsy moth outbreaks, long-term regional impacts on merchantable volume may be minimal (Gansner et al. 1993).

7.2.2 Damage to Non-native Tree Species

Fast-growing non-native tree species (e.g., eucalyptus, pine, cypress, spruce) are frequently planted in the Southern Hemisphere and elsewhere. These plantations often exhibit exceptionally high growth increment and their economic success can, at least in part, be attributed to the fact that trees are growing largely pest free (Liebhold 2012). These plantations are thus particularly sensitive to the introduction of non-native pests. Various introductions of insects and pathogens have seriously affected such plantations in the past century. For example, the most damaging pest of non-native pine plantations in the Southern Hemisphere is probably the European sirex woodwasp, *Sirex noctilio* (Fig. 7.3). However, only damage records in specific stands or areas are available (e.g., mortality rates of 30 % in New Zealand in 1946–1951; 40 % in Tasmania and up to 75 % in Victoria, Australia, between 1932 and 1979; 60 % in Brazil in 1989). In Southern Australia between 1987 and 1989, an outbreak of *S. noctilio* caused the death of 5 million trees with a value of AUS$10–12 million (CABI 2015), but such estimates are calculated using the volume-times-price method, which does not provide a meaningful quantification of economic impact, as described previously.

The green spruce aphid is one of the few species for which data are abundantly available. *Elatobium abietinum* originates in Central Europe where it occurs on *Picea abies* and has been introduced in many parts of the world, affecting both native and non-native spruce stands and plantations. In the UK and Northern Europe, it causes extensive defoliation of Sitka spruce, *Picea sitchensis*, severely reducing height increment by 20–60 % in the year of attack. Similarly, defoliation also decreases diameter increment for 7–8 years, with a mean reduction of 18.5–40.5 %. Even moderate defoliation can cause increment loss in some spruce species (CABI 2015). In Iceland, damage was so severe that initiation of new spruce plantations has largely been abandoned in southern regions (Halldórsson et al. 2003). Interestingly, although in Europe *E. abietinum* rarely kills trees, it has devastated natural stands of *P. englemannii* and *P. pungens* in the interior southwest USA. In New Zealand, tree mortality was also observed, and the aphid is considered to be the main factor preventing spruce being used as a production species in the country (CABI 2015).

Eucalyptus is one of the most widely planted tree genera worldwide (Branco et al. 2015). Various species are planted for pulp and other purposes in all tropical and warm temperate climates. In the past 20–30 years, almost all plantation regions have suffered from a series of invasions by insects originating from Australia (Branco et al. 2015). Damage has often been very serious but, here again, precise

Fig. 7.3 Pine plantation damage by sirex woodwasp, *Sirex noctilio*, in Australia (Photograph by Dennis Haugen, Bugwood.org)

data are scarce and limited in time and space. For example, in southwestern Spain, the cost of damage caused by the Australian longhorn borer, *Phoracantha semipunctata*, on timber yield losses, plus the costs of disposing of non-usable timber, were estimated at more than US$9 million in 1983, and US$7 million in 1984, for an area of 300,000 ha of eucalyptus plantations (Branco et al. 2015). In Galicia, Spain, the snout beetle, *Gonipterus platensis*, was estimated to reduce tree growth by 30 %, causing an economic loss of US$10.5 million annually. In Portugal, the same insect decreased wood volume (projected to 10 years of age) by 51 % in the affected areas in 2004–2006, with losses increasing exponentially with tree defoliation, by up to 43 % and 86 %, corresponding to 75 % and 100 % defoliation, respectively (Branco et al. 2015).

These and other pests have also caused serious problems to eucalyptus forestry elsewhere. In some areas, damage was so severe that planting of susceptible eucalyptus species was abandoned or greatly decreased, such as in New Zealand following the establishment of the eucalyptus tortoise beetle, *Paropsis charybdis*, and other insects and pathogens of Australian origin (CABI 2015). In the absence of precise data on economic losses, the abandonment of commercial tree species because of pests is a good indication of the economic importance of the damage. Another example is provided by cypress plantations in eastern Africa. In this region, damage from the cypress canker, *Lepteutypa cupressi*, led to the replacement of *Cupressus macrocarpa* by *C. lusitanica*, which in turn became severely affected by the introduced cypress aphid, *Cinara cupressivora*, in the 1980s (Cock 2003). Several studies attempted to estimate the economic damage of the latter species and two other invasive conifer aphids in eastern Africa, the pine woolly aphid, *Pineus boerneri*, and the pine needle aphid, *Eulachnus rileyi*, (Cock 2003). In 1991, it was estimated that, up to 1990, *C. cupressivora* had killed trees worth US$44 million and was causing an additional loss of a further US$14.6 million per year through reduction in annual growth increment. The two pine aphids caused a loss of US$2.4 million per year in the region by reductions in the annual growth increment. These figures were considered conservative because they did not include the impact of the aphids on indigenous tree species or allow for any subsequent mortality from *C. cupressivora*. In Kenya, another study estimated that *C. cupressivora* had the potential to kill up to 50 % of all cypress trees during the 30-year harvest cycle.

It should be noted that many insect pest problems in non-native plantations have been solved through the introduction of natural enemies from the area of origin of the pests. For example, the aforementioned beetles, *P. semipunctata* and *Gonipterus* spp., are successfully controlled by egg parasitoids and, to a lesser extent, populations of *C. cupressivora* in East Africa have also been reduced by a parasitoid (CABI 2015). *Sirex noctilio* has been controlled to varying degrees in New Zealand and Australia by introductions of a nematode and parasitoids. Changes in silvicultural practices have also greatly contributed to reducing impacts, particularly in New Zealand.

Plantations of non-native trees are also very sensitive to tree pathogens. A recent example is provided by the Japanese larch, *Larix kaempferi*, widely planted in the British Isles for timber production but also for landscaping and recreational purposes. Since 2009, a widespread dieback and mortality was reported in various parts of the UK and Ireland. Up to 2010, 2400 ha, or about 0.6 million mature larch, were affected. The disease was caused by *Phytophthora ramorum*, an invasive pathogen already known as the cause of “Sudden Oak Death” in western USA (Brasier and Webber 2010; CABI 2015). Trees in affected plantations are felled to minimise further spread, both to forests and to susceptible heathland vegetation. This development could therefore have a significant impact on local economies and Britain’s strategic reserve of timber (Brasier and Webber 2010).

Another older case of an invasive pathogen affecting non-native plantations in Europe is that of the white pine blister rust, *Cronartium ribicola*. In addition to its damage on native five-needle pines in North America as already mentioned, it also eliminated plantations of the American white pine, *Pinus strobus*, in Europe in the nineteenth to twentieth century. In this case, the abandonment was also motivated by the fact that the disease was also seriously threatening cultivated *Ribes* plantations, in particular black currant, as the fungus requires the two hosts to complete its development (Maloy 1997; CABI 2015).

7.3 Impact on Non-wood Forest Products

A variety of other marketable products, such as nuts, berries, and seeds, game animals, mushrooms, oils, medicinal plants, tannins, peat, and forage are often harvested from forests and have considerable value. Their availability can also be affected by pests, but quantitative data are even scarcer than for wood.

Probably the best data on NWFP losses are from conifer seed orchards. Commercial seed production in the European seed orchards is largely affected by non-native seed chalcids of the genus *Megastigmus*, and especially by the American Douglas-fir seed chalcid, *M. spermotrophus*. Douglas-fir seeds for reforestation are sold at a price of approximately 6000 €/kg, but chalcid infestation may decrease the number of healthy seeds by as much as 95 % (Auger-Rozenberg and Roques 2012). The recent arrival of the western North American conifer seed bug, *Leptoglossus occidentalis*, decreased the seed yields in Douglas-fir and pine seed orchards in France by as much as 25.7 % and 15 %, respectively (Lesieur et al. 2014) (Fig. 7.4).

Wild fruits for human consumption can also be affected by forest pests. The strong decline in the production of edible nuts of the stone pine, *Pinus pinea*, observed all around the Mediterranean Sea, is attributed in large part to the arrival

Fig. 7.4 *Leptoglossus occidentalis* feeding on a pine cone (Photograph by Vincent Lesieur)

of *L. occidentalis*. Roversi et al. (2011) mention an unpublished study in an Italian forest measuring that 80 % of the 2-year-old conelets aborted, but large-scale assessments of the effect of the bug on seed production decline are still lacking.

Chestnut production, both in orchards and forests, has been devastated by two Asian invaders, the chestnut blight, *Cryphonectria parasitica*, and the chestnut gall wasp, *Dryocosmus kuriphilus*. In the first half of the twentieth century, almost all mature American chestnut trees were killed by chestnut blight (CABI 2015). The tree now survives as small understory trees. The disappearance of chestnut from American forests also affected the production of other NWFP, such as tannic acid used in leather production. In Europe, the pathogen has been less destructive but, recently the European chestnut has been strongly affected by the arrival of the chestnut gall wasp with losses in nut production as great as 80 % (Battisti et al. 2014).

7.4 Conclusions

There is no doubt that invasions of non-native invertebrates and pathogens can have dramatic economic and ecological impacts on trees and forests. However, direct impacts on market forest resources may sometimes be largely overestimated. Although there are numerous cases of serious impact on tree mortality or tree growth, we are aware of just a few cases where a pest invasion has actually reversed the profitability of forest production. Examples of such reversals include plantations of spruce in southern Iceland and New Zealand, as a result of invasion by *Elatobium abietinum*, and the abandonment of white pine plantations in Europe because of *Cronartium ribicola*, and of several eucalyptus species in New Zealand following the invasion of Australian insects and pathogens. There are numerous reasons why impacts may sometimes be exaggerated. First, for most species, a true assessment of pest species across entire regions over many years is often missing. Such assessments are necessary to form a reliable characterisation of the economic impact of an invading species over an extended period of time (Epanchin-Niell and Liebhold 2015). Second, studies that quantify impacts simply as total numbers of trees or volume killed are inadequate for evaluating the ultimate impacts of a pest on the forest, because between the time of tree mortality (or loss of growth) and harvest, trees in a stand will grow and compensate, at least partly, for mortality or growth loss (Holmes et al. 2009). Thus, simply multiplying the volume of trees killed by its value is completely inadequate for estimating impacts. Impacts on non-market values are undoubtedly highly important, especially when native trees are affected, and fully justify measures put in place to prevent and manage non-native pests (Aukema et al. 2011). However, methods need to be developed to quantify and aggregate market and non-market impacts caused by forest non-native pests.

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Chapter 8
Interference of Non-native Species with Fisheries and Aquaculture

Rodolphe E. Gozlan

Abstract Fisheries and aquaculture in developing countries are primarily a way of producing and providing daily food for millions of the world's poorest people and thus contribute significantly to the fabric of local economies. In other countries, fisheries are also valued for sport fishing activities. However, these types of both food and sport activities rely heavily on the use and thus the introduction of non-native species. Although this is true for both marine and freshwater species, it is far more prevalent in the freshwater fish farming trade than across all other taxa. Asia has used the potential of available species cultured abroad more than any other region in the world, but as most of the cultured species are Asian, this still represents a small proportion of their fisheries and aquaculture economic activity. The proportion of species farmed that are non-native is the greatest in North and South America, Europe, and Oceania (mean = 36 %, 35 %, 43 %, and 34 %, respectively). In terms of production alone, Europe and the former USSR represent the largest production of non-native species (i.e., 62 % of world non-native production, all taxa included). It is extremely difficult to objectively evaluate the cost of non-native species on ecosystem services and the cost of non-native fish species as part of the production of fish for food, which represents about 95.3 % of the global non-native aquatic species production across the world (>81 M tonnes/year) and barely reaches €0.04 M/year. With a growing human population, new challenges are on the horizon, notably the increase and diversification of production using novel technologies (e.g., GMOs) whilst limiting negative side effects and additional costs.

Keywords Aquatic • Biodiversity • Cost • Disease • Ecosystem services • Fish • Plants • Shellfish • Socio-economy

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8.1 Introduction

Many developing countries still rely on freshwater fisheries as a source of food, with 6 % of the world's annual animal protein consumption estimated to be sustained by freshwater fishes (FAO 2012) as it is the main source of animal protein for low-income families (Zhao et al. 2015). The overwhelming majority of freshwater fisheries (i.e., 94 %) are located in developing countries (FAO 2012). In addition to food, these fisheries provide a livelihood for millions of the world's poorest people and thus significantly contribute to the fabric of local economies through the export commodity trade, tourism and recreation. In the Mekong River basin, for example, about 55 million people rely on freshwater fish for food (about 56.6 kg/person/year) and income (Baran et al. 2007). These fisheries constitute the daily exploitation of wild freshwater shellfish, invertebrates and fish stocks. These are often artisanal and sold locally for daily food. They can also be combined with growing ponds, where juveniles are collected in the wild but grown in simple cages that allow more sustainable management of stocks and production. These activities directly rely on wild, uncontrolled production of the offspring (Zhao et al. 2015) and, as such, they represent a significant threat to the natural resource with most wild fisheries near their maximum sustainable levels of exploitation.

These fisheries often rely on the use of locally present native species. However, translocation across river basins has been practiced for centuries, leading to confusion over what is native or non-native (Zhao et al. 2015). For local fisheries stakeholders, the origin of the fisheries production is of limited interest if it responds to local demand and economic needs. Therefore, there is very little legislation regarding the management of fisheries in developing countries and its application is highly flexible—in other words, free market economy rules apply. In other places, fisheries are managed for sport fishing rather than for their nutritional value, as in Europe and North America, where rivers and reservoirs are actively managed to provide sporting activities, including fishing. The underlying business plan is the sustainability of fish populations with large specimens, mostly predators, with either a 'catch-and-release' or 'put-and-take' policy. Thus, most introduced non-native species in these type of fisheries have sporting potential. A typical example is the introduction of the brown trout, *Salmo trutta*, across all continents except Antarctica (McIntosh et al. 2011). Today, established *S. trutta* populations still exist throughout Africa, the Americas, Asia, Australasia, and the sub-Antarctic islands (the Falkland and Kerguelen Islands).

The majority of marine fisheries do not rely on non-native species although there are some exceptions, for example, the introduction of the red king crab, *Paralithodes camtschaticus*, in Norway, where it is now very widespread around the Barents Sea. This limited level of intentional introduction of non-native species in support of marine fisheries results from the sea being an open system that does not guarantee that resources will remain locally distributed to be exploited.

This chapter characterises and illustrates through the use of case studies, the main interference of non-native species with fisheries and aquaculture practices.

This review includes the impact of non-native species on fisheries and aquaculture and also the impact of non-native species used for fisheries and aquaculture.

8.2 Overview of Non-native Aquatic Species Use in Fisheries

Most sought after fish, invertebrate and mollusk species have already been introduced outside their native distribution and have contributed to the phenomenon of biotic homogenisation (Gozlan et al. 2010). From the range of cultured fish species that could be introduced in a particular world region, between 15 % and 27 % of farmed fish are in effect introduced (Fig. 8.1; mean 22.8 %; standard deviation (SD) 3.62). This range is a lot more variable for crustacean species (mean, 17.4 %; SD, 6.84) and a lot less variable for mollusk species (mean, 5.1 %; SD, 5.01). These data reflect the mollusk aquaculture sector, which relies far more on native species than either the fish or crustacean sectors, possibly for cultural dietary reasons.

Fifty-four percent of all species farmed in the world are native to Asia. Asia has used the potential of species cultured abroad more than any other region but, as most cultured species are Asian, this still represents a small proportion of their fisheries and aquacultural economic activity (Fig. 8.2). Thus, in absolute numbers, Asia is

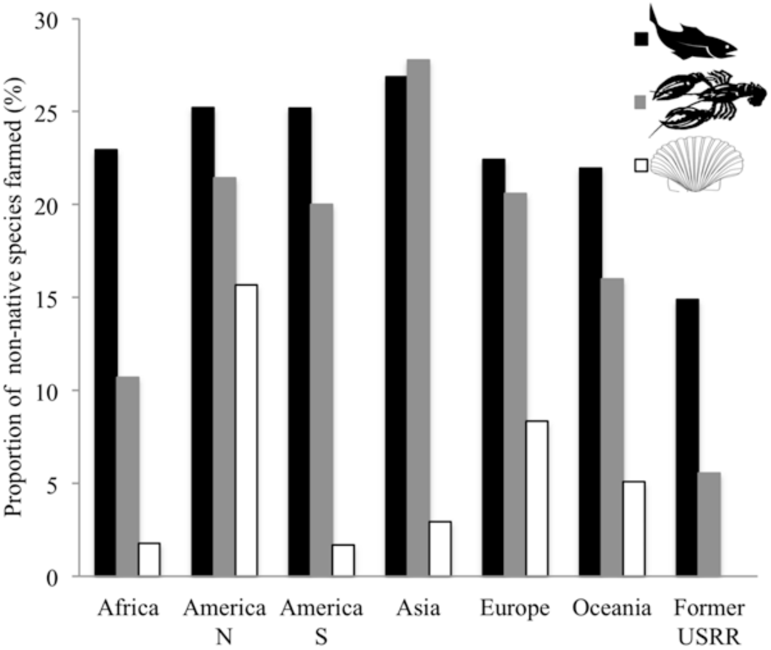

Fig. 8.1 Percentage of non-native species farmed in each continent from the total number of non-native species that could be farmed in a particular taxonomic group (Source*:* FAO database on introductions of aquatic species http://www.fao.org/fishery/dias/en)

Fig. 8.2 A rich selection of freshwater fish on sale by artisanal fishmongers at the main fish market in Wuhan (China) (Photograph by Rodolphe E. Gozlan)

one of the world's regions that farms the least non-native species (i.e., 27 %) (Figs. 8.1, 8.3). The proportion of non-native species used in aquaculture is the greatest in North America (mean, 36 %; SD, 8.5), South America (mean, 35 %; SD, 25.4), Europe (mean, 43 %; SD, 14.5) and Oceania (mean, 34 %; SD, 23.1) (Fig. 8.4).

It is often stated that the aquaculture sector will have to continually rely on non-native species to increase aquaculture production. However, the market analysis in terms of non-native species alone is fairly deceptive when one looks at actual volume of production (Fig. 8.5). Here, Europe and the former USSR represent the

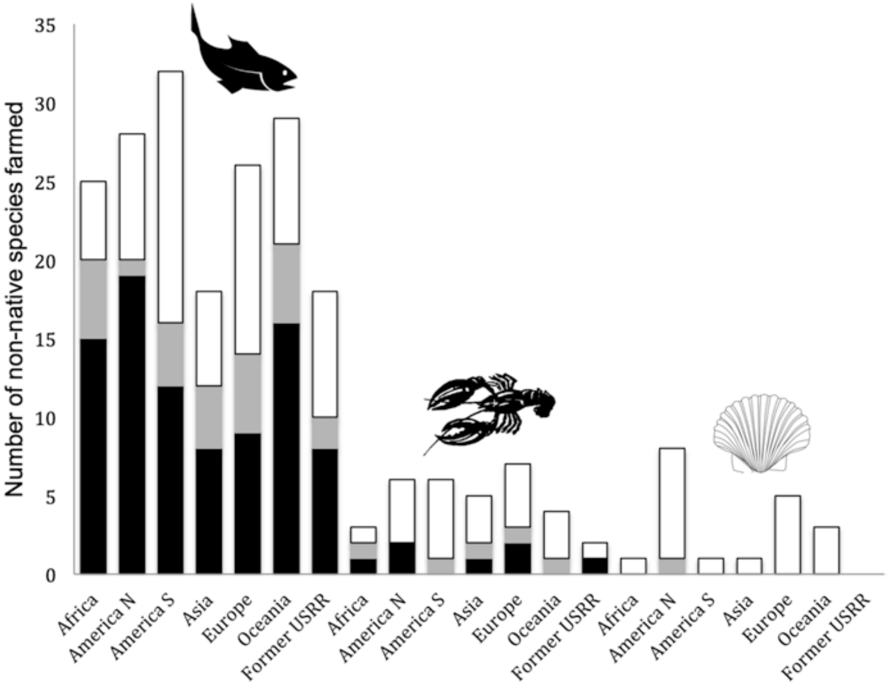

Fig. 8.3 Breakdown per taxonomic group of non-native species across aquatic habitat. *Black bars* represent strict freshwater species, *grey bars* are freshwater and brackish species and *white* bars are for species that have part of their life history in seawater (Source*:* FAO database on introductions of aquatic species http://www.fao.org/fishery/dias/en)

largest production of non-native species (i.e., 62 % of world non-native production, all taxa included). Annual non-native production for the former USSR reaches about 3 million tonnes (Mt) and relies on 18 non-native species (mostly fish), whilst the European non-native production is 2.4 Mt and comprises 38 non-native species. Therefore, in terms of number and volume of production combined, European aquaculture relies most on non-native species.

8.3 Landscape of Non-native Aquatic Species Production in Fish Farms and Fisheries

The largest freshwater fish production includes the farming of four carp species (grass carp, *Ctenopharyngodon idellus*; common carp, *Cyprinus carpio*; silver carp, *Hypophthalmichthys molitrix* and bighead carp, *Hypophthalmichthys nobilis*), which alone account for more than 6.6 Mt. However, only about 0.5 % is produced as non-native species, as most of the production is concentrated in Asia and the

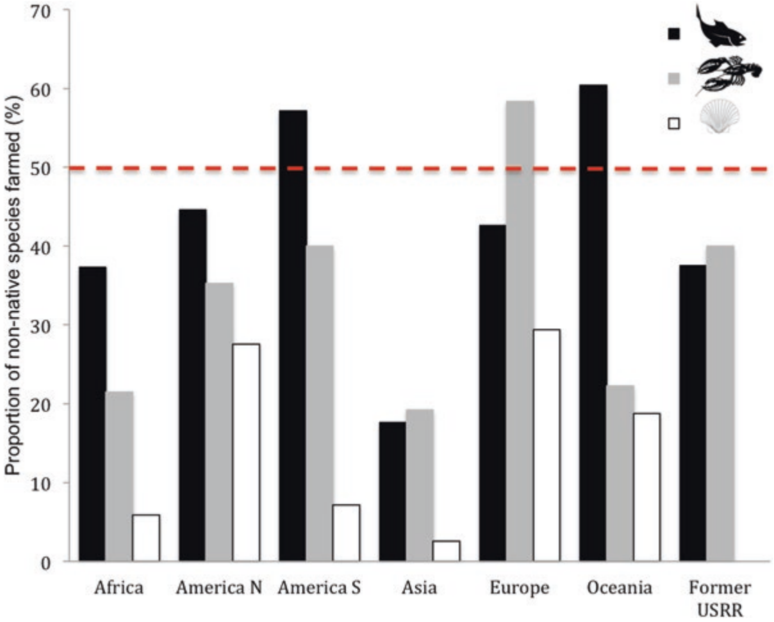

Fig. 8.4 Proportion in percentage of non-native species farmed over the total number of species farmed in each world region and for each taxonomic group. The *red dashed line* represents half the species farmed (Source*:* FAO database on introductions of aquatic species http://www.fao.org/fishery/dias/en)

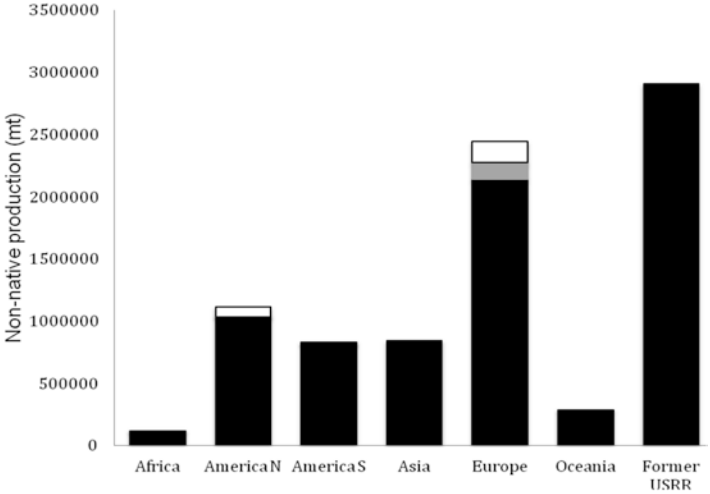

Fig. 8.5 Distribution of non-native aquatic species production across several world regions: *white* for mollusks, *grey* for crustaceans, *black* for fish (Source*:* FAO database on introductions of aquatic species http://www.fao.org/fishery/dias/en)

former USSR where these species are native. The largest salmonid production comprises rainbow trout, *Oncorhynchus mykiss*; Atlantic salmon, *Salmo salar*; and sea trout, *Salmo trutta*; which together account for about 700,000 tonnes annually with about 50 % being produced as a non-native species, mostly in South America (e.g., Chile). Here, it becomes apparent that there are no consistent patterns in terms of volume of production and percentage of production being produced outside the species native distribution. In effect, geographic use of a fish species is often linked to (1) ancestral practices, such as pond culture in Asia that can be traced back to around 3300 years ago with *C. carpio* being the first domestic fish in the world (Zhao et al. 2015); (2) trade pathways, such as the translocation of Chinese carp species across the former USSR countries; or (3) 'new' market prospects with, for example, the production of salmonids in Chile that started in the mid-1980s and now represents a US$3 billion/year aquaculture industry employing around 35,000 people. Conversely, most marine fish farming industry focuses on the use of native species. Only red seabream, *Pagrus major*, is farmed in Europe as non-native species and turbot, *Psetta maxima*, is farmed in South America with an annual production of 24 tonnes. This preference is probably the result of the greater distribution range of marine fish species.

The majority of crustacean species cultivated are marine species (i.e., 63 %) dominated by species of shrimp (e.g., Penaeidae, $n = 22$), representing an overall annual production of about 750,000 tonnes, but only 125 tonnes of which is produced using non-native species. This production of Penaeidae as a non-native species concerns the aquaculture of the kuruma prawn, *Penaeus japonicas*, in Europe. Here again, the geographic location of the production is driven by market forces, in particular cheaper labour, within the native range, which limits the export of penaeid production. Some species of Palaemonidae, such as the Asian giant river prawn, *Macrobrachium rosenbergii*, that is farmed in brackish water, have been introduced around the world to Africa, North and South America, European peripheral territories and the former USSR, but they still only represent about 18 % of total production (~21 tonnes). Thus, out of non-native crustacean production, the non-native part is only marginally significant for European production but still relatively minor compared to the volume of fish production (Fig. 8.5).

Mollusk aquaculture species are mostly marine (97 %), including a range of clams, mussels, oysters and abalone species. The only significant non-native production concerns the aquaculture of the Pacific cupped oyster, *Crassostrea* gigas, (226 thousand tonnes; 23.5 % of the overall production), mostly in North America and Europe but also to a lesser extent in Africa and Oceania. This aquaculture sector does not heavily rely on non-native species (Figs. 8.1, 8.3). On average, only 5 % of available non-native species are exploited in any one region of the world (SD, 5.01), which is relatively low compared to the crustacean sector (mean, 17.4 %; SD, 6.84).

8.4 Negative Impact on Fisheries and Aquaculture

Along with increasing global trade, exchange of species and techniques and know-how, fisheries and aquaculture production have suffered from accidental species and pathogen introductions that have limited production. Most of the accidental species that have been introduced and that have impacted the functioning of fisheries and aquacultures, can be categorised as ecosystem engineers (i.e., species that modify the local ecosystem by their biological function), species responsible for biofouling (i.e., species that affect infrastructures) or pest/pathogen species.

8.4.1 Non-native Ecosystem Engineers

The great majority of non-native species that have affected fisheries and aquaculture are typically ecosystem engineer species and in general aquatic macrophytes, which are difficult to eradicate as a few introduction events can rapidly lead to large clonal populations (Wang et al. 2005). The majority of these introductions are through the ornamental trade, with species such as curly water weed, *Lagarosiphon major*; parrot feather, *Myriophyllum aquaticum*; and New Zealand pygmy weed, *Crassula helmsii*; which impact fisheries with dense mats or strands with closed canopies that rapidly change fisheries habitats and could lead to major oxygen depletion responsible for fish kills. Species such as Himalayan balsam, *Impatiens glandulifera*, that increase riverbank instability, erosion, and sediment drift also negatively impact fish spawning grounds. However, some introductions are unintentional (e.g., alligator weed, *Alternanthera philoxeroides*, and purple loosestrife, *Lythrum salicaria*, (Wang et al. 2005). In the marine environment, for example, the invasion of *Caulerpa taxifolia* in the Mediterranean as an escapee from the Monaco aquarium has seen the decline of several important fisheries habitats such as seagrass, *Posidonia oceanica*, meadows. In all cases, these non-native macrophytes have had greater impacts on the fisheries than on the aquaculture sector per se. In addition, the introduction of invertebrates or mollusks (e.g., *Corbicula* sp. and the zebra mussel, *Dreissena polymorpha*) presents a considerable biofouling risk for local infrastructures (Mackie and Claudi 2010). Several other non-native aquatic phyla have been introduced worldwide, including amphibians and mammals, which have had an impact on fisheries through a rapid change in the ecosystem. For example, the coypu, *Myocastor coypus*, or the North American beaver, *Castor canadensis*, have direct impacts on fisheries habitats because they generate significant changes in flow patterns, riparian vegetation and structure of the riverbank (Catford 2017).

8.4.2 Pests and Pathogens

Despite all of the potential negative impacts resulting from the introduction of non-native species to fisheries and aquaculture, the greatest threat remains the introduction of pest species and pathogens (Peeler et al. 2011). A typical example is the introduction of a non-native predator of oyster, *Urosalpinx cinerea*, that was initially introduced from the US Atlantic Coast with the imports of eastern oysters to the Pacific Coast. Also, the Japanese oyster drill, *Ceratostoma inornatum*, which was introduced along with oyster seed from Japan, has particularly impacted newly seeded Pacific oyster crops. Just after the Second World War, a new set of policies from the US government that required a thorough inspection of oyster seed shipments from Japan, along with a transition of the industry to hatchery-produced seed, prevented further accidental introductions through the shellfish industry.

In addition to the introduction of pest species, the role of non-native species in the emergence of novel diseases has clearly been established through the increased geographic distribution of pathogens and parasites and also as facilitators of host-switching (Peeler et al. 2011). There have been many examples of pathogen/parasite introductions and dramatic effects on aquatic wildlife and biodiversity, with some having a direct impact on fisheries. For example, *Anguillicola crassus*, a parasitic nematode, directly impacted wild populations of the European eel, *Anguilla anguilla*; *Bonamia ostreae*, a parasitic protist, led to the dramatic decline of stocks of the flat oyster, *Ostrea edulis* and *Aphanomyces astaci*, the crayfish plague, was responsible for the severe decline of the native European crayfish, *Astacus astacus*. In all three cases, the pathogens were accidentally introduced into fisheries but their emergence was underpinned by different mechanisms. For example, *A. crassus* is a typical case of a host-switching from Asian eels, *Anguilla japonica*, imported to Germany (Koops and Hartmann 1989), *B. ostreae* emerged in Europe with the reintroduction from the USA of native *O. edulis* spats into France and Spain (Comps et al. 1980) and *A. astaci*, although probably initially introduced via ballast water, truly emerged when the non-native host signal crayfish, *Pacifastacus leniusculus*, was introduced to Europe during the 1960s in support of crayfish fisheries (Alderman 1996).

8.5 Case Studies

There is a wide range of examples that could illustrate interference of non-native introductions with fisheries and aquaculture. As such, it is always difficult to justify a selection. The aim here was to provide a range of detailed examples across major phyla and systems; thus, this is not an exhaustive record of potential impacts arising from non-native species introduction, but rather a general overview.

8.5.1 Fish

Tropical Rabbit Fish With the effect of climatic change on marine ecosystems, more and more tropical species have seen an expansion of their geographic range and have now conquered new temperate areas in response to increased sea temperature in some localities. In addition, man made structures, such as the Suez Canal, have bridged tropical and temperate seas, allowing more species from the Red Sea to establish in the Mediterranean. A good example of such climatic and human-mediated invasion is the establishment of a large population of rabbit fish, *Siganus luridus* and *Siganus rivulatus*, in part of the eastern Mediterranean Sea. These fish species are a typical example of ecosystem engineers and thereby have greatly impacted algal beds (i.e., 65 % less abundant) and the benthic biomass (i.e., 60 % reduction) of rocky reefs. These fish are herbivores feeding on algal forests and seagrass meadows (Vergés et al. 2014), which are habitats that are among the most productive and rich in species in temperate coasts. The implication for local fisheries is still not yet established, but the observed decline in carnivorous fishes in rabbit fish-occupied regions (biomass and diversity) could be driven in part by a reduction in prey abundance. This type of emerging ecological impact from non-native marine species range shifts is predicted to become more frequent in connected tropical-temperate sea regions (Ling et al. 2008).

Mozambique Tilapia The introduction of the Mozambique tilapia, *Oreochromis mossambicus*, throughout the world is a great example of non-native species introduction in support of ecosystems services, such as fish farming and insect or weed control. This species has specifically been selected for its robustness to environmental conditions (i.e., general hardiness, fast growth, ease of breeding and potential to benefit from organic waste) and broad dietary tolerance. Thus, it has often been introduced into habitats that have been subjected to severe environmental changes, such as dam construction sites or large-scale irrigation projects. Therefore, it could be considered as a pioneer species, thriving in areas that display severe habitat damage and where natives are already at risk (Canonico et al. 2005). A high number of *O. mossambicus* populations are now well established and integrated into local fish communities. This is also suspected to have locally resulted in the decline of commercial and traditional fisheries including species extinctions, changes in water quality and impact on macrophytes (Witt 2017). However, although it has been reported by the FAO that, in the Philippines, introduced Mozambique tilapia have displaced preferred species of the mullet *Mugil cephalus*, brackish water shrimp, *Penaeus merguiensis* and milk fish, *Chanos chanos*, in brackish water fish ponds, there is currently no scientific evidence to support this view. In effect, the main tilapia fish farming in the Philippines is supported by the Nile tilapia, *O. niloticus* and not *O. mossambicus*, as the latter was considered too dark in colour and too small by consumers and thus had a poor market image (Dey et al. 2000). In addition, *C. chanos* and *P. merguiensis* are, respectively, the second and fourth most produced species in the Philippines. Thus, one has to be very careful in assessing the true

Fig. 8.6 The topmouth gudgeon, *Pseudorasbora parva*, has been responsible for a severe decline of wild fisheries and aquaculture stocks (Photograph by Rodolphe E. Gozlan)

impact of a non-native species on ecosystems and or ecosystem services in developing countries as it is often blurred by a range of other socioeconomically driven environmental impacts that are typical of these regions and supported by few scientific studies (Gozlan 2015).

Topmouth Gudgeon This is an unusual case of interference from a non-native species with fisheries and aquaculture because the introduction of the topmouth gudgeon, *Pseudorasbora parva*, although driven by fisheries and fish farming, was accidental (Fig. 8.6). In effect, a combination of political commercial partnerships in the former USSR countries and the expansion of fish farming in Europe fuelled one of the fastest invasions by any fish, with about five new countries being invaded every decade (Britton and Gozlan 2013). Initial introductions were driven accidentally via Chinese carp fish farming (65 % of introductions), recreational fishing (22 %), the ornamental fish trade (9 %), and natural dispersal (1 %) and further dispersal then occurred primarily from natural dispersal (72 % of the cases) and angling (25 %). Although reduced production of carp species was observed when *P. parva* was present on the farm, mostly as a result of feeding competition (Gozlan 2015), the impact of *P. parva* itself on fisheries and fish farming remains limited. However, the identification of *P. parva* as a healthy carrier of *Sphareothecum destruens*, an infectious pathogen, is a concern as this non-native pathogen has been responsible for mass mortalities in a range of fish species (e.g., salmonid, cyprinids, percids) in Europe and in the USA. It has also recently been confirmed to have led to the sharp decline of several endemic species in the wild (i.e., 80 %), some of which were part of local fisheries and even linked to sea bass mortalities in Mediterranean fish farms. So, although the fish itself is a limited menace for fisheries and fish farms, the pathogen that it carries is one of the most well supported cases of the impact of a non-native species on ecosystem services.

Common Carp The first introduction of the common carp, *Cyprinus carpio*, into Europe dates back to post-Roman times. A more contemporary set of introductions has occurred in North, Central and South America, the Middle East, Africa, Australia, and Oceania. Today, only about 1 % of *C. carpio* is produced outside its native range (FAO 2012). In aquatic systems, increased turbidity results from *C. carpio* feeding as it resuspends sediment and nutriments while uprooting macrophytes (Weber and Brown 2009). This reduction in light availability furthers the decline in the abundance of submerged macrophytes and leads to blooms of cyanobacteria (Williams and Moss 2003; Hinojosa-Garro and Zambrano 2004). However, controversy remains as to whether observed environmental degradation results entirely from *C. carpio*. There are examples where even high *C. carpio* densities (i.e., 480 individuals/ha) have not led to declines in native species biomass (Barthelmes and Brämick 2003). It seems that high species richness and deeper lakes could mitigate the impact of *C. carpio* (Carey and Wahl 2010). It is obvious that in clear shallow lakes with a high diversity of submerged macrophytes, the introduction of carp is likely to result in severe changes in the ecosystem (Miller and Crowl 2006). In habitats that are already degraded, either through reduction in water quality or by overfishing, *C. carpio* introductions are unlikely to lead to major impacts (Hicks et al. 2011).

8.5.2 Crustaceans

Waterflea The small planktonic cladoceran *Cercopagis pengoi* can reproduce parthenogenically (asexually) or sexually, thus providing adaptability to environmental conditions and allowing a small number of introduced individuals to rapidly colonise new areas. This is another good example of a pioneer species with resting eggs resistant to freeze drying, desiccation and predation by fish. Their dispersal is facilitated by the presence of a barbed caudal spine which allows attachment to fishing lines/nets, bird feathers and vegetation, but they are also distributed through ballast water. The full impact of *C. pengoi* on the food web has not yet been extensively studied, but based on laboratory, bioenergetic, and physiological studies, it seems that *C. pengoi* feeds on small herbivorous zooplankton and thus reduces their abundance. For example, in Lake Ontario, predation from *C. pengoi* led to a steady decrease in zooplankton after it became established (Laxson et al. 2003). A more recent study has shown that, in Lake Michigan, temporal and spatial niche segregation between native and non-native predatory cladocerans has allowed their coexistence (Cavaletto et al. 2010). It has also been shown that *C. pengoi* has rapidly been integrated into the diet of local native fish species (Gorokhova et al. 2004). Therefore, the main interference with fisheries and fish farms is the intense clogging of nets and fishing equipment, leading to economic losses in some fish farms.

8.5.3 Mollusks

Pacific Oyster *Crassostrea gigas*, which has been introduced in more than 20 countries worldwide for aquaculture purposes, is a typical ecosystem engineer that could locally lead to deep changes in ecosystem function, in part by increased filtration of planktonic food sources, but also through the formation of oyster reefs. These types of ecological changes have antagonistic outcomes on native species that are beneficial for some and negative for others. A thorough assessment of the Pacific oyster's impact on the whole ecosystem has been carried out for the Wadden Sea (i.e., north of Europe). The conclusion of the report stated that no species losses were yet observed and that native blue mussels are coexisting with Pacific oysters on reefs as they offer an alternative habitat to species traditionally found on blue mussel beds (i.e., epibenthic and endobenthic species). Studies in other locations have found that oyster reefs hosted higher densities of invertebrates (e.g., crabs, bivalves, worms) (Escapa et al. 2004). However, it is often suspected that introduction of the Pacific oyster has led to the introduction of additional non-native species that come through the same pathways as contaminants on oyster shipments (Ruesink et al. 2005). Conversely, in the Wadden Sea, many non-natives that could have been introduced along with oyster imports have not established sustainable populations (Nehls and Büttger 2007). In addition, Wolff and Reise (2002) have shown that there is no strong evidence that oyster imports have lead to the introduction of shellfish diseases. Because of its economic value, the management of the Pacific oyster as a non-native species is unique. For example, in Washington State alone, Pacific oyster aquaculture is worth $85 million and in several parts of the state, shellfish aquaculture is the single largest employer. Thus, throughout the Pacific Northwest, the introduction, spread and establishment of this species is often encouraged. Once established, if environmental conditions are favourable to Pacific oysters, it is generally impossible to contain. Because of the very high densities of Pacific oysters in Port Stephens, New South Wales (NSW, Australia), its culture has been allowed since 1990, leading to a well-established industry worth around US$1.5 million annually. At the same time, the Pacific oyster has been listed under the *Fisheries Management Act 1994* as a Class 2 Noxious Fish in all NSW waters, except in Port Stephens, thus showing the whole complexity of labelling non-native species as a pest species (NSW DPI 2013). It also illustrates quite well how difficult it is to reconcile ecological and economic perspectives when it comes to fisheries and aquaculture.

8.5.4 Echinoderms

North Pacific Seastar The northern Pacific seastar, *Asterias amurensis*, is likely to have been introduced into Australia via ballast water from Japan, where it is a native species. It has now established a large population in southeastern Australia, including

Tasmania and Victoria, specifically in Tasmania's Derwent River estuary and Victoria's Port Phillip Bay. It is known to be a voracious predator with a broad diet, but would favour mussels, scallops, and clams. Where first detected in Port Philip Bay, population estimates reached about 12 million specimens in around 2 years. As such, it is considered as a pest with local negative impact on native shellfish farming and fisheries through predation and fouling of salmon traps and scallop and oyster lines (Ross et al. 2004). However, this economic impact has not yet been measured or quantified although the North Pacific seastar was introduced in Tasmania in 1986. Removal trials have shown that the physical removal of the North Pacific seastar was probably the most effective, safe, and socially acceptable method of control, compared to chemical or biological methods (Thresher and Kuris 2004).

8.5.5 Protists

Gymnodinium catenatum This planktonic flagellated protist (i.e., dinoflagellate) produces a neurotoxic poison that contaminates shellfish and could affect consumers. Currently, there is little evidence to characterise its native range and the only clear evidence of an introduction is into Australia and New Zealand, most likely via the ballast water of ships from Japan (Bolch and de Salas 2007). Reports have mapped it locally over a few hundred kilometres along the coastlines of all continents (Bolch and de Salas 2007). The main interference of *G. catenatum* with aquaculture and fisheries is as a result of paralytic shellfish poisoning (PSP). The economic costs of PSP, although not specific to *G. catenatum*, have been estimated annually at about US$50 million for the US (Hoagland et al. 2002) and US$0.75 million in Australia. These costs are not directly linked to human poisoning, as monitoring programs are extensive in many affected countries, but to loss of income resulting from harvest closures and reduced confidence in seafood products by consumers. For example, the Huon estuary in Tasmania, which has been severely affected by *G. catenatum*, is no longer economically viable for oyster and mussel production because of the high risk of PSP, which can persist over long periods of time.

8.6 Economic Cost

In economic terms, the cost to Europe from all introduced non-native species has been estimated at about €12 billion, mostly from terrestrial species. For example, the annual economic cost *of Anguillicoloides crassus* has been estimated at about €32.5 million and the cost for *Aphanomyces astaci* at about €0.21 million (Kettunen et al. 2009). However, figures on economic costs from non-native species remain limited and vary greatly from one geographic region to another and between taxa. Attempts to extrapolate the costs greatly inflate estimates, as shown for example, by the difference in the annual cost in Europe of *A. astaci* introduction, which has a real cost fixed around €0.21 million and an extrapolated cost of €70 million. Taking this into account, the estimated cost to European fisheries of non-native species has been estimated at about €314 million/year, which is marginal when compared to the overall estimated annual cost of €12 billion across all non-native species in Europe (Kettunen et al. 2009). The mean cost for each aquatic taxonomic group is €4.46 M ± SE 5.37 for plants, €16.35 M ± SE 19.53 for invertebrates (crustaceans + mollusks), €0.04 M ± SE0.03 for vertebrates and €34.80 M ± SE 49.96 for pathogens.

8.6.1 Perspectives

It is extremely difficult to objectively evaluate the cost of non-native species on ecosystem services. The overall cost of invasive species on fisheries and aquaculture must be balanced with the profit generated by the production of the species. For example, the production of non-native aquatic species across the world is dominated by the production of fish for food, representing more than 81 million tonnes per year—about 95.3 % of the global non-native aquatic species production across the world (Fig. 8.5). In contrast, the annual cost from aquatic vertebrates in Europe barely reaches €0.04 M on average. So from a business perspective alone, this is a fairly profitable market with limited side effects, particularly as the economic cost is generally not covered by the fish farming industry but instead by governmental agencies (i.e., taxpayers' money).

The biggest risk for the fisheries and fish farming industry in general remains the risk of pathogen introductions. This is an even greater risk when farming non-native species as the introduction of non-native pathogens along with non-native fish stocks could have a severe effect on other farmed native species that are not well prepared to handle novel pathogens, as is clearly seen in the annual economic cost of introduced non-native pathogens in Europe (e.g., about €139 M). This cost includes prevention of pathogen introduction, such as *Gyrodactylus salaris* with an annual cost of more than €106 M; or the cost of managing past pathogen introductions, such as *Aphanomyces astaci*, the crayfish plague, with an annual cost of €0.21 M; or *Anguillicola crassus*, an eel swimbladder nematode, that has an annual cost of more than €32 M. This costing is not specifically restricted to aquaculture and fisheries activities, but also includes prevention, early detection and rapid eradication and management by local, governmental and European agencies. Thus, there are no reliable figures about the effective economic cost directly imputed to both ecosystem services and generated by the farming or introduction of non-native species.

8.6.2 Policies

In terms of policies regarding non-native species, there is often a conflict between regulations dealing with the prevention and management of the introduction and spread of invasive species and the economic drivers that benefit from the commerce of non-native species. A good example is Regulation No. 1143/2014 of the European Parliament adopted on the 22nd of October 2014. The core aspect of the regulation provides a framework to deal with the prevention, management and spread of invasive non-native species in Europe. However, article 2 deals with the scope of the regulation and clearly indicates that the regulation does not apply to genetically modified organisms, pathogens that cause animal disease, harmful organisms listed in Annex I or Annex II to Directive 2000/29/EC, species listed in Annex IV to Regulation (EC) No. 708/2007, microorganisms manufactured or imported for use in plant protection (Regulation (EC) No. 1107/2009), or, finally, to microorganisms manufactured or imported for use in biocidal products (Regulation (EU) No. 528/2012). The latter two regulations deal directly with the important European trades including the phytopharmacetical industry and the biocidal industry. In other words, the regulation does not aim to limit European trade, even if that trade includes the introduction and movement of non-native species (or similar, such as GMOs), but instead only targets species that have not been deliberately introduced into the wider environment.

The non-native species used in European aquaculture that escape the foregoing have all been listed as part of Annex IV to Regulation (EC) No. 708/2007. This comprises a list of ten non-native species, including eight freshwater fish species (rainbow trout, *Oncorhynchus mykiss*; brook trout, *Salvelinus fontinalis*; common carp, *Cyprinus carpio*; grass carp, *Ctenopharyntgodon idella*; silver carp, *Hypophthalmichthys molitrix*; big head carp, *Aristichtys nobilis*; large-mouth bass, *Micropterus salmoides* and Arctic char, *Salvelinus alpinus*) and two species of mollusks (Pacific cupped oyster, *Crassostrea gigas* and Manila clam, *Ruditapes philippinarum*). All of these non-native species support relatively important production with, for example, the annual production in Europe of the three carp species (i.e., *C. carpio*, *H. molitrix*, and *H. nobilis*) equating to more than 7 million tonnes, with the production of *O. mykiss* alone being more than 3 million tonnes. It is also interesting to note that none of the economic costs associated with the non-native species listed in Annex IV have been estimated in the economic study carried out by the Institute for European Environmental Policy (Kettunen et al. 2009), with the exception of *C. gigas* with an annual economic cost estimated at about €1 M.

8.6.3 Point of View

Most farmed species or species that are intentionally introduced to a fishery provide positive socioeconomic outcomes (Zhao et al. 2015). Removing non-native species from the fisheries sector would have a significant negative impact on socioeconomic indicators, in particular for fish aquaculture in the former USSR and Europe and to a lesser extent in North and South America and Asia (see Fig. 8.4). However, although the contribution of non-native fish species is more limited in Africa and Oceania, on a local level constraining legislation to prevent the farming of these species may have a significant socioeconomic impact, particularly in rural communities that are often already on the brink of poverty. In economic terms, the figures on economic profits from fisheries-related non-native species remain scarce. For example, it has been estimated that in Europe the introduction of the Chinese mitten crab, *Eriocheir sinensis*, generates about €4.5 million/year, while the introduction of red king crab, *Paralithodes camtschaticus*, in Norway is worth about €6.8 million with an export value of about €12.8 million (Kettunen et al. 2009). Locally, the landing value of *P. camtschaticus* can be close to the traditional cod fisheries. In addition, in Italy alone the introduction and exploitation of the Manila clam, *Tapes philippinarum*, has generated an income of about €178 million/year, second only to the largest world producer, China. Fisheries and aquaculture form the basis of a business model that leads to both employment and the production of wealth, and responds to consumer demand both locally and also on a broader scale through international trade for fish, crustaceans, and mollusks.

8.7 Conclusions

In conclusion, fisheries and aquacultures all over the world rely heavily on non-native species, and their economic benefits greatly outweigh the economic cost for the farmers and fisheries managers. Some unexpected impacts have been experienced (see case studies for examples), but the industry has been relatively prompt in finding solutions, such as the oyster fisheries in the US. In many parts of the world, where fisheries and fish farming are an essential source of cheap protein for the local population, there is little incentive to reduce the volume of non-native species in the production and new potential markets may arise with the farming of genetically modified organisms. New challenges are thus on the horizon for these ecosystems services, notably the increase and diversification of production using novel technologies while limiting negative side effects and additional costs.

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Chapter 9
Impacts of Non-native Species on Livestock

Nigel P. French

Abstract Livestock systems have both benefited from and been harmed by the deliberate and unintended introduction of non-native species. The introduction of non-native pests and pathogens into livestock populations has resulted in severe economic, welfare, and public health consequences. These impacts include: competition for resources; livestock mortality and disease; costly eradication programmes; ongoing surveillance to ensure border and post-border biosecurity; and the burden of zoonotic pathogens on human health. In common with other systems, the impact of non-native invasions is determined by the ability of the pest or pathogen to enter the system (incursion), multiply and spread (expansion), and become established and endemic (persistence). The determinants of incursion, expansion, and persistence depend on the pest or pathogen and the livestock system invaded and include climate change, habitat encroachment, the effectiveness of border and post-border biosecurity, and the onset of acquired immunity in the host population. Examples of non-native invaders discussed in this chapter include vertebrate pests (e.g., mammals competing for resources), invertebrate pests (e.g., ectoparasites and vectors for microbial pathogens), and pathogens (e.g., viruses and bacteria). Advances in genome sequencing, and the development and application of models that combine epidemiology and evolution, offer new insights into invasion dynamics and new approaches to reducing the impacts of pests and pathogens on livestock populations.

Keywords Incursion • Epidemiology • Expansion • Human health • Persistence • Livestock • Pathogens • Parasites • Pest • Well-being

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9.1 Introduction

Most humans rely on the farming of non-native species for the bulk of their food supply, and food-producing livestock systems are often established by the introduction of non-native species. Hence, the focus of this chapter is on the impact of relatively recent invasions on established livestock systems (including ruminants, pigs, and poultry); recognising that both the invading species and the livestock hosts are usually non-native. The impacts, both positive and negative, are briefly considered, followed by a description of the negative effects of pests and pathogens on agricultural production, animal welfare, and human health. A framework for invasions into livestock systems is presented, followed by some examples of pest and pathogen invasions that have had a major negative impact on livestock farming around the world.

9.2 Overview of Impacts

9.2.1 Negative Impacts of Non-native Species on Livestock

Invasions of non-native pests and pathogens into livestock systems have increased mortality and morbidity and reduced productivity. As a result, rigorous biosecurity and disease control measures have been established, both at borders between countries and post-border within countries, to prevent the incursion, expansion, and persistence of invading species into livestock systems. Historically, there have been notable and well-documented incursions of vertebrate and invertebrate pests and microbial pathogens that have devastated livestock production and affected farming systems, from small-holder subsistence farming to large-scale livestock production. The direct effects of pests and pathogens on livestock systems can be measured in terms of their direct economic and animal welfare impacts and, as many commensal microorganisms and livestock pathogens also affect humans, the effect of zoonotic transmission on public health.

9.2.2 Positive Impacts of Non-native Species on Livestock

The introduction of some non-native species has had a considerable, positive effect on livestock farming. For example, deliberate and accidental introductions of non-native plants such as ryegrass, *Lolium* spp., and clover, *Trifolium* spp., into pastoral ecosystems has increased pasture yield and quality, resulting in higher feed-conversion rates and productivity in ruminant livestock (Driscoll et al. 2014). Another example is the introduction of dung beetles into Australia (subfamily Scarabaeinae) to break down cattle faeces that would otherwise accumulate and reduce pasture productivity.

9.3 Economic, Welfare, and Human Health Impacts of Non-native Species on Livestock

9.3.1 Economic Impact of Non-Native Species on Livestock Production

Non-native pest and pathogen invasions can cause significant losses to agriculture, food, and tourism industries. In the United Kingdom (UK), the foot-and-mouth disease (FMD) incursion and subsequent large-scale outbreak in 2001 resulted in estimated losses of £3.1 billion to agriculture and the food chain, and a similar amount to the tourism industry (Thompson et al. 2002). Despite an extensive programme of compensation, it was estimated that the loss to farmers represented about 20 % of their total income. Further, effects on market access of trans-boundary diseases, such as FMD, are also wide ranging, costly, and often of long duration (Fig. 9.1).

The direct economic cost of pest and pathogen invasions is attributed to a number of outcomes including: disease-associated mortality and morbidity; production losses such as a drop in milk yield in dairy animals; slower growth rates in meat-producing animals; the costs of treating sick animals; and the cost of control measures such as preemptive culling and vaccination. Even an unrealised threat of invasion can incur significant costs to livestock production, for example, the efforts required to prevent the invasion of New and Old World screw worm flies, *Cochlimyia hominivorax* and *Chrysomia bezziani*, into Australia require expensive surveillance activities (Fruean and East 2014). Further, the threat of deliberate release can be costly, for example, the release of FMD virus on an offshore island in New Zealand in 2005, despite being a hoax, was estimated to cost the Ministry of Agriculture and Forestry more than NZ$2 million.[1] These incidents lead to considerable concern about the potential deliberate release of invasive species as an act of bioterrorism.

The introduction of non-native invasive weeds has also resulted in negative impacts on livestock production, as discussed in the following section.

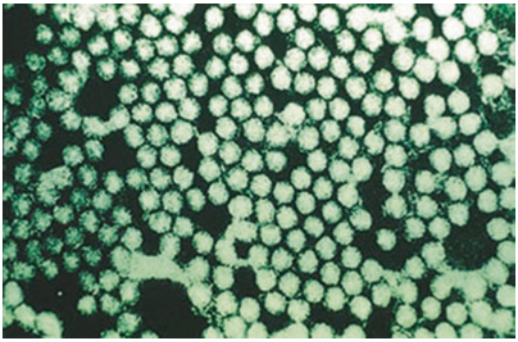

Fig. 9.1 Electron micrograph of the foot-and-mouth disease virus, a picornavirus. Foot-and-mouth disease is an important trans-boundary disease of cloven-hoofed animals [Photograph from Wikipedia/FBI (public domain)]

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[1] http://www.nzherald.co.nz/waiheke-island/news/article.cfm?l_id=364&objectid=10127415

9.3.2 Impact of Non-native Species on Animal Welfare

The incursion of pests and pathogens into previously unexposed, and hence immunologically naïve, populations can result in severe morbidity and mortality, with obvious impacts on animal welfare. As examples, vertebrate pests such as rabbits, *Oryctolagus cuniculus*, can compete for resources, resulting in starvation and death; ectoparasite infestations such as the sheep scab mite, *Psoroptes ovis*, can cause considerable distress and severe pathology (Berriatua et al. 2001); and an outbreak of a viral disease, such as FMD, in a naïve population can result in a wide range of symptoms, including painful ulcerative lesions in the oral cavity and feet in a high proportion of animals.

Introductions of non-native invasive weeds have adversely affected livestock production, health, and welfare. Included are weeds that have impacts arising from selective grazing, direct toxicity to grazing animals, limitation of pasture production, and costs of weed control. For example, fireweed, also known as Madagascar ragwort, *Senecio madagascariensis*, is a native of southern Africa that has subsequently been introduced into South America, Australia, and Hawaii (Mader et al. 2016). This weed has resulted in production losses from competition for resources and livestock mortality resulting from the ingestion of toxic pyrrolizidine alkaloids contained within the plant. Further examples of invasive weeds with impacts on productivity and animal health and welfare include other ragwort species (*Senecio* spp.), thistles (*Cirsium* spp.), and barley grass (*Critesion* spp.).

9.3.3 Impact of Non-native Pathogens on Human Health

It has been estimated that more than two-thirds of human pathogens are transmitted between animals and humans (Taylor et al. 2001; Rabitsch et al. 2007), and many of these are transmitted from livestock via food, water, and direct contact. Some of the most important food-borne pathogens, such as *Campylobacter jejuni* and Shiga toxin-producing *Escherichia coli* O157 (STEC O157), have little or no effect on their livestock reservoir, but can cause severe illness and result in a major burden to public health in many countries. This concern has led to stringent and costly food safety measures, and potential barriers to trade between countries, further adding to their economic burden. For example, STEC O157 has been introduced into many countries (Strachan et al. 2015), most likely through the importation of ruminant livestock, causing large-scale food-borne outbreaks and environmentally acquired sporadic cases of gastroenteritis, often associated with life-threatening complications (Majowicz et al. 2014).

9.4 Determinants of the Impact of a Non-native Species on Livestock Populations

Non-native invasions into livestock systems share many features in common with invasions into plant and wildlife ecosystems (Morand 2017); their impact is determined by their ability to overcome barriers to introduction and establishment (Mack et al. 2000). For a non-native species to affect a livestock population, first it must enter the agricultural ecosystem (introduction or incursion). Following incursion, the subsequent impact is determined by a number of factors including the size of the founding population, the capacity for population expansion, and the likelihood of persistence.

The processes of incursion, expansion, and persistence depend on a number of drivers (for examples, see Table 9.1), some of which are unique to livestock systems, whereas others are common to multiple systems. For example, incursion and persistence of a pest or pathogen into plant, wildlife, and livestock systems will depend on the effectiveness of border biosecurity and the number and frequency of introductions (propagule pressure). Similarly, parasite vector range expansion can facilitate the invasion of pathogens into both plant and animal systems. However, the opportunities for local and long-range expansion of invasive species may be greater in animal systems, particularly where there is a large volume of animal movements between premises through a highly connected network (Robinson et al. 2007). Conversely, the likelihood of incursion, expansion, and persistence of microbial pathogens is limited in livestock and wildlife systems by the onset of targeted acquired immunity resulting from both natural infection and the use of vaccines.

If the invading 'founder' population is small and at low density there is a usually high probability of fade-out (extinction), which would limit the impact of a non-native invader. For vertebrates and invertebrates in particular, a lower fitness associated with a low number or density of introductions can increase the likelihood of extinction. Invading populations can avoid extinction by adapting and recovering (evolutionary rescue), adding new immigrants (demographic rescue), or by enhancing genetic variation that facilitates adaptation (genetic rescue) (Kanarek et al. 2015). Therefore, in common with other systems, the likelihood of incursion, expansion, and persistence into livestock systems is greater if there are repeated introductions, underlining the need for effective border and post-border biosecurity measures.

As many of the high-impact invaders into livestock systems are parasites, including macroparasites (e.g., arthropods) and microparasites (e.g., bacteria and viruses), an assessment of their impacts requires the application of ecological and epidemiological frameworks and models (Anderson and May 1991). Many important features of the ecology and epidemiology of livestock parasites are common to invasions in other systems, including: parasite population dynamics; the interactions between species, such as host, macroparasite vector, and microparasite (including their coevolution); and the effects of the new environment on parasite populations (Mack et al. 2000).

Table 9.1 Drivers for incursion, expansion, and persistence of pests and pathogens into livestock systems

Driver	Incursion	Expansion	Persistence	Specific examples
Climate change	Expansion of insect vector range results in incursion.	Temperature and humidity more suitable for pathogen multiplication.	Increased virus persistence over winter.	*Culicoides* spp. and bluetongue virus in Europe.
Habitat encroachment, wildlife migration, and livestock intensification	Emergence of new pathogens from wildlife into livestock systems as a result of changes in farming practice.	Repeated introductions between livestock and wildlife increases transmission and expansion.	Movement of infected livestock facilitates regional spread and persistence.	Emergence of Nipah virus in Malaysia and Singapore and the role of migratory wild birds in the dissemination of avian influenza viruses.
Border and post-border biosecurity	Breaches of border biosecurity increase likelihood of incursion and poor post-border biosecurity allows for geographic spread.	Repeated incursions increase likelihood of successful establishment by increasing genetic fitness.	Inadequate monitoring and control post-border results in endemic state.	Tick-borne diseases such as *Theileria orientalis*.
Global trade in animals and animal products	Increased movement across borders increases likelihood of incursion.	Repeated incursions increase likelihood of successful establishment by increasing genetic fitness.		Spread of African Swine Fever and the introduction of food-borne pathogens such as non-typhoidal *Salmonella* and Shiga-toxin-producing *E. coli* into livestock systems.
Increased size and density of livestock host population		Intensification of livestock production provides a large number/density of naive susceptible individuals which allows population expansion.	New susceptibles introduced into the population are sufficient for persistence and an endemic state.	Nipah virus in Malaysia and Singapore.

Deliberate release	Introduction of animals for biocontrol or hunting.	Repeated introductions allow population expansion caused by increased genetic fitness.	Persistence is the goal of deliberate release.	Brushtail possums (*Trichosurus vulpecula*) in New Zealand and European rabbits (*Oryctolagus cuniculus*) in Australia.
Acquired immunity in livestock hosts		If immunologically naïve, pathogens are more likely to replicate in livestock hosts, resulting in outbreaks of disease. If cross-immunity is conferred by a related pathogen then outbreaks are less likely, and the severity of clinical signs is likely to be lower.	Influx of immunologically naïve hosts through birth, immigration and waning immunity enables persistence. Vaccination would reduce the number of susceptibles and reduce the likelihood of persistence.	Control and potential global eradication of peste des petits ruminants (PPR) by mass vaccination.
Post-border intervention	Prevents incursion into new areas.	Insect vector local eradication programmes reduce likelihood of vector and vector borne pathogen expansion.	Culling and ring-vaccination reduce likelihood of persistence.	Rinderpest eradication and the control of African Swine Fever and Foot and Mouth Disease.

9.4.1 Incursion

The probability of incursion into a livestock system, defined as the probability a pest or pathogen enters a population regardless of whether they become established, is determined by a number of factors such as the effectiveness of border and post-border biosecurity measures and the frequency of movement of carrier livestock, pests, and pathogens into a defined area. Incursion risk will be reduced if there are effective points-of-entry detection and eradication programmes in place. Such systems need to be responsive to changes in climate, land use, agricultural demography, and trade patterns.

Changes in land use and wildlife habitat encroachment have led to the incursion of new diseases that have affected both livestock production and public health. For example, in Malaysia the previously unknown Nipah virus was first isolated from pigs and then humans with symptoms of high fever, muscle pain, and severe encephalitis. Epidemiological studies revealed the maintenance host to be fruit bats feeding on flowers and mangoes in groves near pig farms. This led to infection in the pig population and zoonotic spread to pig farmers, resulting in high mortality among those affected (Luby and Gurley 2012). The initial incursion may have been self-limiting, but there is evidence that repeated subsequent introductions led to persistence in a growing pig population. Subsequent movement of infected pigs, including ‘fire sales’ in response to clusters of human cases, further exacerbated the spread into southern Malaysia and Singapore, allowing expansion and persistence of the virus (Pulliam et al. 2012).

9.4.2 Expansion

Following an incursion, the probability that the pest or pathogen can multiply and expand its range depends on a number of factors. For vertebrate and invertebrate pests, the initial viability and growth potential of the population depends on the presence of mating pairs or pregnant females, and the resources available. Range expansion will depend on the presence of physical barriers (e.g., natural barriers such as rivers or mountain ranges), and the potential for hitchhiking on vectors (e.g., the movement of animals carrying helminth parasites and parasite vectors).

For microbial pathogens, the probability of an incursion resulting in a sustained outbreak or epidemic is determined by factors such as: the size and/or density of the susceptible population; the initial number of infected animals; the onset of a protective immune response; pathogen-induced mortality; the infectivity of the pathogen (i.e., the probability of transmission given contact between susceptible and infected individuals); the rate of contact between individuals in the population; and the implementation of targeted interventions (such as culling of infected animals or vaccination). These factors are components of the ‘basic reproduction ratio’ (R_o), which for microparasites, such as viruses and bacteria, is defined as the average number of secondary infections that would result from a single infected individual introduced into a population in which every animal was susceptible. Thus, R_o= 1 is an important threshold used in modelling the spread of infectious diseases: if $R_o >$ 1, then invasion and persistence is likely; if $R_o < 1$, then invasion is less likely, and the pathogen will not persist in the population.

The same concept can be scaled up to consider transmission between farms and provide a framework for understanding incursion, expansion, and persistence into a livestock system, as illustrated in Fig. 9.2. Scenario A represents a situation where border biosecurity measures are sufficient to prevent any incursion. In contrast, scenarios B and C represent situations where invasion is possible, but either $R_o < 1$ (scenario B) or interventions are put in place to reduce R_o to <1 (scenario C). In both scenarios B and C, initial expansion may occur and, in the case of scenario B, it may go undetected, but in neither case does incursion lead to persistence. In this scenario, expansions may be detected as outbreaks or epidemics, but these are self-limiting. In scenarios D and E invasion, expansion, and persistence occur because R_o remains >1, either because of inadequate intervention (scenario D) or no intervention (scenario E). In scenarios D and E, initial outbreaks or epidemics lead to a persistent endemic state and/or epidemic cycles.

Epidemiological models of the expansion and spread of pathogens, between animals and between farms, have been deployed to inform contingency planning and control policy in the face of pest and pathogen outbreaks. Such an approach provides a priori guidelines on the relative merits of control policies, such as ring vaccination and culling in the event of a new incursion (Keeling et al. 2003). A similar approach, using intrinsic and effective rates of population growth and dispersal rates, could be used to model the potential impacts of invasion of an arthropod vector or non-native parasite (Atzeni et al. 1997).

9.4.3 Persistence

A pest or pathogen can invade a livestock system, rapidly multiply and cause disease, but then be eliminated without human intervention. The reasons for such a decline and ‘fade out’ include the exhaustion of resources needed to sustain the pest or pathogen. For example, in the case of an infectious disease, the decline in the number of susceptible animals below a critical level, as the result of high mortality or the onset of acquired immunity, would lead to a self-limiting epidemic. If $R_o > 1$ and there is a replenishment of susceptible individuals resulting from, for example, the birth of naïve animals or the loss of acquired immunity, then persistent cycles of infection and/or a persistent ‘endemic’ state may result. An endemic state can result in persistent negative impacts, but this may be attenuated by a reduction in pathogen virulence, and a state of endemic stability associated with lower impacts on health and productivity (Coleman et al. 2001).

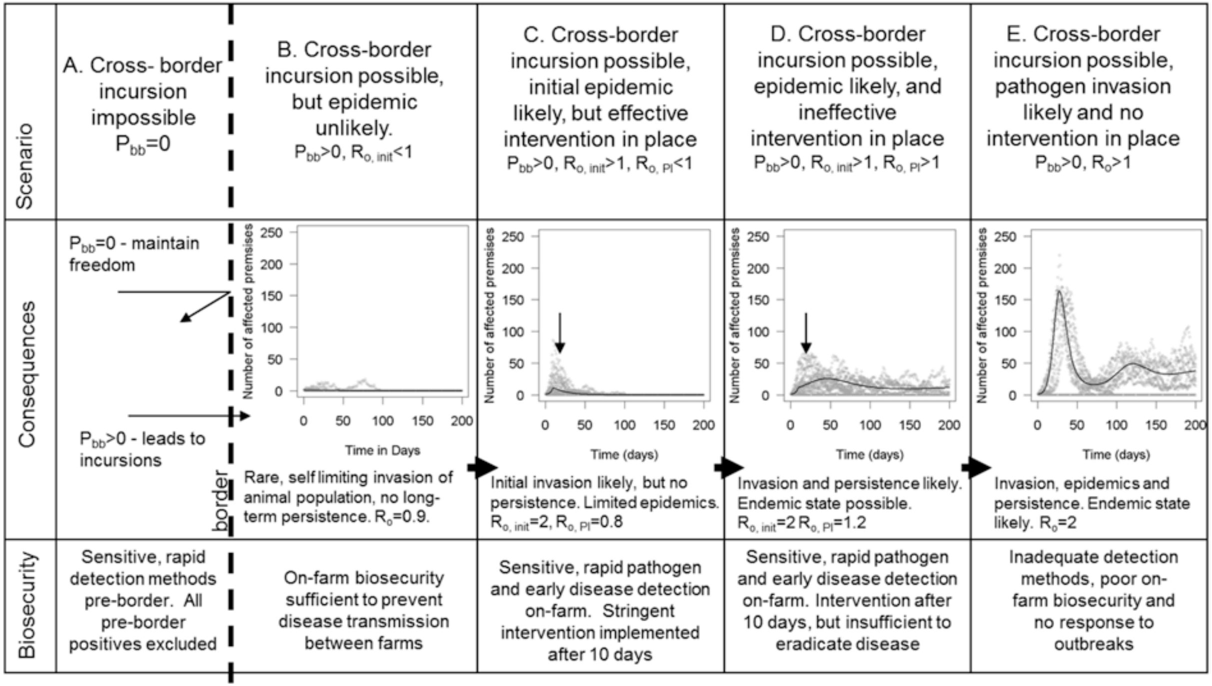

Fig. 9.2 A model-based framework for illustrating incursion, expansion, and persistence of a non-native pathogen into a livestock system. Scenarios A–C represent effective biosecurity, whereas D and E illustrate poor biosecurity, leading to pathogen invasion and an endemic state. P_{bb} is the probability of a cross-border incursion, R_o is the basic reproduction ratio, $R_{o,\text{init}}$ is the basic reproduction number of the pathogen in the animal population without specific control measures in place: this is the average number of secondary cases (farms) that would be infected from a single infected case in a fully susceptible population. $R_{o,PI}$ is the basic reproduction number post intervention. The graphs show the output from deterministic (*solid line*) and stochastic (*grey dots*) models that capture the transition of farms between states; from susceptible to infectious, infectious to recovered, and from recovered back to a susceptible state (SIRS model), under each scenario in a population of 1000 farms (Taken from French et al. 2007)

9.5 Examples of Invasive Pests and Pathogens and Their Impact on Livestock Populations

9.5.1 Vertebrate Pests as Resource Competitors

The introduction of invasive vertebrate animals into livestock farming environments can have a major impact on production as a result of direct competition for resources. For example, the introduction and spread of feral European rabbit, *Oryctolagus cuniculus*, populations into Australia in the 1800s, notably an introduction of 24 rabbits for hunting in 1859, have resulted in major losses in terms of crop production and the effects of erosion and reduction in the productivity of grazing areas used for livestock production. Rabbit competition with livestock for pasture has resulted in a reduction of livestock densities, reduced wool production and poor wool quality, lower weight gains and reproduction rates, and a greater impact of drought on stock mortality. Higher predator numbers, such as the red fox, *Vulpes vulpes*, attributed to increased rabbit populations have also been cited as a cause of reduced lamb survival. As a result, competition for grazing by the feral European rabbit is now listed as a ‘key threatening process’ in the Threatened Species Conservation Act in New South Wales, Australia.[2]

9.5.2 Vertebrate Pests as Vectors for Invertebrate Pests and Pathogens

Deliberate or accidental introduction of wild and domestic animals into livestock farming areas have resulted in the introduction of new pests and pathogens into naïve populations and provided a population of reservoir hosts that can act as vectors for disease-causing agents. For example, the Australian brushtail possum, *Trichosurus vulpecula*, was introduced into New Zealand in 1858 with the aim of establishing a trade in possum fur. The population rapidly expanded, and current estimates are of a population size around 30 million. Although they do not directly compete for livestock resources, they have had a major impact on livestock production as a result of their role as a reservoir for *Mycobacterium bovis*, a cause of tuberculosis (TB) in cattle and humans (Fig. 9.3). The importance of possums as a host for bovine TB emerged in the 1960s, although possums, cattle, and TB were all introduced into New Zealand in the 1800s. Concerted and costly control efforts, such as systematic and intensive testing of cattle, coupled with culling of infected animals and movement controls, have reduced long-term transmission within cattle, and intensive lethal control of possum populations has reduced the problem to a relatively small number of *M. bovis*-infected possum populations. Controlling TB in introduced wildlife in New Zealand currently costs ~$NZ50 million per annum (Nugent et al. 2015).

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[2] http://www.dpi.nsw.gov.au/agriculture/pests-weeds/vertebrate-pests/pest-animals-in-nsw/rabbit-control

Fig. 9.3 Multiple lesions caused by *Mycobacterium bovis* in the lungs of an Australian brushtail possum, *Trichosurus vulpecula*, captured in New Zealand (Photograph by Kyle Richardson)

9.5.3 Invertebrate Pests

9.5.3.1 Direct Disease-Causing Parasites

A number of invertebrate parasites have the potential to cause devastating outbreaks if they invade previously unexposed livestock populations: these include endoparasites such as helminth worms (which may be introduced by vertebrate vectors) and ectoparasites (which may be introduced by vertebrate vectors or airborne spread). Examples of non-native direct disease-causing parasite invasions include the introduction and post-eradication reintroduction of the sheep scab mite, *Psoroptes ovis*, into the UK (French et al. 1999). The welfare impactions of direct disease-causing ectoparasites, such as scab mites, blowflies, and screw-worm flies, can be severe and result in major production losses.

9.5.3.2 Parasite Vectors

Invertebrate ectoparasites such as ticks and biting flies are capable of transmitting a wide range of pathogens. Tick-borne diseases are a major cause of livestock production losses worldwide, and can be introduced into naïve populations through the introduction of cattle infested with the *Theileria*-infected ticks. A recent example is the outbreak of *Theileria orientalis* in New Zealand (McFadden et al. 2011).

Climate change has been implicated as a major driver of range expansion for parasite vectors and incursion into new livestock populations. An example is the effects of climate change on the expansion of the northern range of a biting midge *Culicoides imicola* since 1998, and increased virus persistence over winter, which led to the transmission of initially six strains of bluetongue virus (BTV) among ruminants across 12 countries in Europe. The spread of BTV 800 km further north in Europe than previously described has disrupted trade in animals and animal

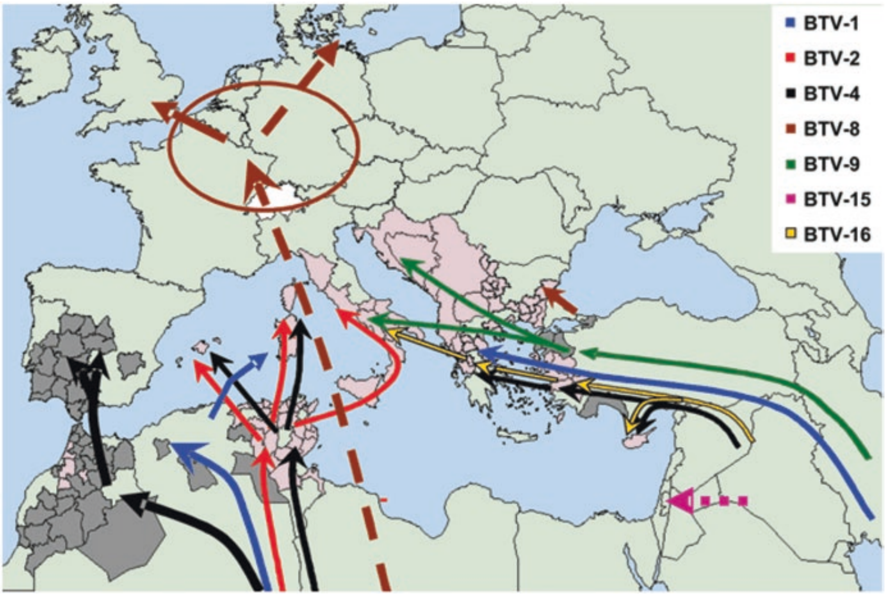

Fig. 9.4 Movement of seven lineages of bluetongue virus (BTV) that have been introduced into Europe from different geographic areas. Their introduction is linked to climate change and range expansion of the biting fly vector, *Culicoides imicola* (From Purse et al. 2005)

products and resulted in the death of more than a million sheep (Purse et al. 2005). In 2006, serotype BTV-8 was discovered in Northern Europe, spreading quickly between Belgium, the Netherlands, and Germany. During the next 3 years, BTV-8 spread to most countries in western and central Europe (Durand et al. 2010) (Fig. 9.4).

9.5.4 Microbial Pathogens

Microbial pathogens continue to be a major source of production loss in livestock systems, and the impacts of examples of viral, bacterial, and protozoan parasites have been mentioned ealier in this chapter. They can be introduced into naïve livestock populations through multiple transmission routes including the movement of domestic and wild animals, humans, and parasite vectors. They can also invade systems as a result of airborne (Konig et al. 2009) and waterborne spread, leading to explosive outbreaks followed by a persistent endemic state.

Examples of invading bacteria include the non-typhoidal *Salmonella* species. The emergence and global spread of *Salmonella enterica* Typhimurium clones, particularly those resistant to multiple antimicrobial agents, such as *S.* Typhimurium DT104, have affected both human and animal health. Recent work combining epidemiological modelling with evolutionary modelling, and applied to the global *S.* Typhimurium DT104 epidemic, has demonstrated the considerable potential these techniques hold for improving our understanding of invasion and transmission dynamics in livestock systems and their impact on human health (Mather et al. 2013). The advent of new genome sequencing technology and improved epidemiological and evolutionary models has also led to a greater understanding of the number and origin of historical invasions of pathogens into livestock systems. By determining the genetic relatedness of microbial pathogens, long- and short-range geographic jumping events can be identified, and by dating the common ancestor of invading populations, the rough timing of biosecurity breaches and subsequent invasions can be determined. These techniques have been used to examine historical events, such as the origin of the 1967/1968 FMD epidemic; a recent analysis revealed multiple introductions over the time period in question (Wright et al. 2013).

In addition to FMD, there are many other examples of ‘trans-boundary’ viral pathogens that cause widespread morbidity and mortality in livestock. These pathogens cross international boundaries through trade-related livestock movements and other pathways, and can lead to major welfare concerns and economic losses. Examples include the now globally eradicated rinderpest (Mariner et al. 2012) and other viral diseases such as African swine fever (ASF) (Sanchez-Vizcaino et al. 2015). ASF was first described in Kenya in the early twentieth century and subsequently spread rapidly to other African countries. Waste used as pig feed that was contaminated with infected pig products spread the disease beyond Africa to Portugal in 1957. Although this initial incursion was controlled, a reintroduction in 1960 spread ASF to the whole Iberian Peninsula and this persisted for more than 30 years. Between 1960 and 1995 the disease spread to other countries in Europe and America (i.e., Brazil, Dominican Republic, Cuba, Haiti). Eradication from these countries has been successful, but the disease still persists in Sardinia. Contaminated pig feed has also been implicated in the more recent spread in 2007 of ASF into Eastern Europe including Georgia, Armenia, Azerbaijan, and the Russian Federation, where wild pigs are also considered to play a role in the epidemiology of this disease. The presence of ASF in East and Central Europe poses a serious risk to other EU countries.

Trans-boundary viral diseases also have major impacts on poultry production and, in the case of avian influenza, on human health. Migratory wild birds and trade in poultry products are considered important for the movement of zoonotic influenza A viruses over wide geographic areas and thus have key roles in the incursion of highly pathogenic avian influenza (HPAI) A H5N1 virus into new areas. More recently, around 2010–2011, a new clade termed 2.3.4.4 emerged in China (Claes et al. 2016) containing strains such as H5N6 and H5N8; the latter subsequently spread between continents via migratory wild birds (Lee et al. 2015). In 2014, H5N8 viruses were identified in Canada and the USA; these subsequently re-assorted with wild-bird influenza viruses and rapidly spread into domestic turkeys and chickens, resulting in the culling of more than 48 million birds, with an estimated loss of $US1.6 billion to the USA economy (Claes et al. 2016).

9.6 Conclusions: Responding to Non-native Pests and Pathogens in Livestock Systems

Many of the mitigation approaches aimed at protecting livestock systems from non-native invasions of pests and pathogens are similar to those developed for other systems, including the design and adoption of risk assessment frameworks, pathway and vector management, early detection, rapid response, and new approaches to mitigation (Mack et al. 2000). Maintaining good biosecurity requires rapid, sensitive detection of invasive species, including pathogens and vectors, and signs of disease in target populations. This is an ongoing exercise in many countries, particularly those that depend on livestock farming for their economic well-being, and an integral part of surveillance and related activities aimed at preventing invasion and persistence of non-native species. Improvements in genome sequencing technology, combined with advances in epidemiological and evolutionary modelling, are providing new tools for understanding invasion dynamics and informing animal and public health decision making. These include decisions concerning the targeting of surveillance activities and the implementation of control measures; such as the reduction or eradication of pest populations, culling and disposal of infected animals, and vaccination. Control strategies informed by epidemiological and evolutionary modelling offer new approaches to reducing the substantial economic, animal welfare, and public health impacts of non-native species invasions into livestock systems.

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Part III

Impacts on Regulating Services

Chapter 10
Displacement and Local Extinction of Native and Endemic Species

Petr Pyšek, Tim M. Blackburn, Emili García-Berthou, Irena Perglová, and Wolfgang Rabitsch

Abstract The observational evidence on non-native plants, mammals, reptiles, fish, mollusks earthworms, and insects as drivers of population declines or extinctions of native taxa suggests that non-native predators are far more likely to cause the extinction of native species than non-native competitors. Notable examples of such taxa include non-native vertebrates and mollusks as mainly predators and plants and insects as mainly competitors. The most vulnerable species are insular endemics, presumably because of the lack of coevolution between introduced pred-

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ator and native prey. Island-like situations contribute to severe impacts because the affected native taxa have nowhere to escape. The presence of dormant stages in plants makes it possible to escape unfavourable conditions over time and might contribute to the lack of clear evidence of native plant species driven to extinction by plant invaders. Overall, robust evidence has accumulated during the past few decades that non-native species are drivers of local and global extinctions of threatened, often endemic, native species.

Keywords Competition • Disease • Endemic species • Invasion debt • Island • Species extinction • Population decline • Predation • Vulnerable species

10.1 Introduction

Biodiversity, the variability among living organisms on Earth, represents the foundation of human well-being by providing different services to mankind (Millennium Ecosystem Assessment 2005), and extinction or deterioration of biodiversity puts the availability of many of these services at risk. The questions of whether, and if so, to what extent, non-native species are generally responsible for population declines or extinctions of native taxa has received increasing attention in the last couple of decades. A number of case studies had strongly implicated non-native species in extinctions of individual species (Bell 1978), or at specific locations (Fritts and Rodda 1998). These observations were followed by data-based analyses and evaluations of available data on causes of population declines and extinction, such as on threatened species in the USA (Wilcove et al. 1998) or species on the IUCN Red List (Gurevitch and Padilla 2004; Bellard et al. 2016). A number of these reports provided evidence implicating non-native species as a driver and a leading cause of native and endemic species extinctions (Blackburn et al. 2004; Clavero and García-Berthou 2005). Nevertheless, other authors have questioned these conclusions (Gurevitch and Padilla 2004; Sax and Gaines 2008).

A wide range of human activities are changing environments around the world, with deleterious effects on the species inhabiting these environments. Examples of these activities include agriculture and aquaculture, carbon emissions into the atmosphere leading to climate change, biological resource use, pollution, and residential and commercial development. These changes need to be taken into account when evaluating the role non-native species are thought to have in causing extinctions, because this role may be based to a large extent on circumstantial evidence. Species declines and extinctions are rarely associated with single driving processes (Bellard et al. 2016), and so it is possible that in many cases, native species declines and non-native species increases are coincidental, arising from simultaneous responses of native and non-native species to other anthropogenic disturbances. Direct causality is generally difficult to prove (Gurevitch and Padilla 2004), and the rigorous experiments that would allow the effects of multiple factors and their interactions to be separated are logistically difficult and therefore largely nonexistent. Several recent authors have argued that the impacts of non-native species as drivers of extinction have been overestimated as a result (Gurevitch and Padilla 2004; Didham et al. 2007). Invasion debts, cumulative effects, or the decoupling of cause and effect by time lags, in combination with shifting baselines of the effect size over time, create further difficulties in evaluating the impacts of invasions (Essl et al. 2015).

Efforts to prevent, control, or mitigate the environmental impacts of these species soak up substantial financial and social resources from conservation organisations and concerned governments. In this chapter, the available evidence on non-native species as drivers of population declines, or extinctions of native taxa, is summarised. The analysis is focused on non-native plants, vertebrates, mollusks earthworms, and insects, but not examples of pollinators, pathogens, and pests to crops and forests, because these topics are presented in other chapters of this book (Fried et al. 2017; Kenis et al. 2017; Morales et al. 2017).

10.2 Invasion-Caused Population Declines or Extinctions

10.2.1 Searching for Patterns Across Taxa: Quantitative Evidence from Large Datasets

Wilcove et al. (1998) were among the first to compile data on threats to a large number of threatened species for a large geographic area in the United States (USA). They identified non-native species as a major driver of threat. Subsequently, Gurevitch and Padilla (2004) focused on the causes of extinctions in the IUCN database, arguing that non-native species were implicated in only a small proportion of extinctions. However, their analysis was shown to be flawed, and greatly underestimated extinctions caused by non-native species, as pointed out by Clavero and García-Berthou (2005). These authors showed that of 680 extinct animal species, causes could be identified for 170 (25 %), of which 91 (54 %) included the effects of non-native species. Globally, non-native species were found to be the most frequent known cause of extinction for birds and the second most frequent for fish and mammals (Clavero and García-Berthou 2005). Revisiting this analysis using updated IUCN Red List data found similar results: non-native species are the second most common threat associated with plant, amphibian, reptile, bird, and mammals species that have gone completely extinct since 1500 AD, and the most common threat associated with extinctions in each of amphibians, reptiles, and mammals considered separately (Bellard et al. 2016). Non-natives had their lowest impact on plant species, where they were only the fourth ranked driver of extinction (Bellard et al. 2016). In a similar analysis of IUCN data for threatened species in Europe, 354 species (of 1872 threatened) were considered to be specifically affected by non-native species, and they represented the third most important cause of threat after dam construction and water management, and agricultural and forestry effluents (Genovesi et al. 2015). A recent global meta-analysis of the ecological impacts of non-native species in inland waters revealed strong negative effects of invaders on native species abundances that were, however, not associated with a decrease in species diversity of invaded communities, suggesting a time lag between rapid abundance declines and local extinctions (Gallardo et al. 2015).

For birds, population declines for 68 of the 98 imperilled species in the USA (Wilcove et al. 1998) were attributed to non-natives. These impacts were mainly caused by non-native predators, which threatened 57 % of the 68 species; by non-native pathogens, affecting 34 % of the 68 species (all in Hawai'i); and by other non-native animals acting as competitors. Evidence for impacts of non-native plants is much weaker. Thus, less than 6 % of imperilled bird species were thought to be declining because of non-native plants as the only factor. However, if non-native plants exerted impacts, it was in the majority of cases in combination with habitat destruction (Wilcove et al. 1998). Evidence for damage to bird populations owing to non-native plants is correlative, and it is unknown whether the non-native plants have had a definitive causal role in the decline of any bird species (Gurevitch and Padilla 2004). Another analysis revealed that the number of non-native mammal species is positively correlated with the proportion of the endemic avifauna lost to extinction across islands worldwide (Blackburn et al. 2004).

Together, these data sets indicate that (i) most imperilled species face more than one threat, and (ii) it is difficult to disentangle proximate and ultimate causes of decline or interactions between different threats (Gurevitch and Padilla 2004). Overall, these studies provide consistent evidence that (iii) non-native species represent a major threat to rare and endemic native species that often leads to extinction. The mechanisms behind these processes are best illustrated by the examples of case studies that follow.

10.2.2 Case Studies of Non-native Plants: Past Population Declines of Native Species Suggest Future Extinctions

Numerous vegetation studies document the retreat of native species from invaded plant communities by competition with the invader (Brewer 2008). Only a few published cases, however, more or less clearly demonstrate the threat of particular plant invaders to specific conservation targets (some examples are listed in Table 10.1).

The paucity of hard evidence that non-native plants drive extinctions of native plant species may be caused by the interaction of mechanism and time. Plants interact primarily through competition, which is a slow and subtle process. Most non-native invasions have only occurred within the last few hundred years, and this may not be sufficient time for the full impacts of plant invasions to have played out, especially given the ability of plants to ride out difficult times in dormant stages. For example, the invasion of the South American native tree, *Cinchona pubescens*, into a formerly treeless environment in the Galápagos Islands decreased the diversity

Table 10.1 Selected studies investigating population displacement of native species caused by invasion

Region	Non-native species (taxon, origin)	Invader group: life history	Native species affected (*endemic)	Displacement/extinction	Suggested mechanism	Source
Galápagos	*Cinchona pubescens* (Rubiaceae); South America	Plant: tree	*Pteridium arachnoideum*, *Cyathea weatherbyana**, *Miconia robinsoniana**, *Pilea baurii**	Cover of most native species decreased by at least 50 %, cover of endemic herbaceous species reduced by 89 %; no species lost at the landscape scale	Increased shade and precipitation	Jäger et al. (2009)
Mauritius (Black River Gorges National Park)	*Psidium cattleianum* (Myrtaceae); South America	Plant: tree	*Ixora vaughani**, *Nervilia bicarinata*, *Chassalia capitata**; understory flora critically threatened (IUCN criteria)	Two species that were presumed extinct and several critically threatened with extinction had recovered following the removal of non-native plants; no species lost	Competitive exclusion	Baider and Florens (2011)

(continued)

Table 10.1 (continued)

Region	Non-native species (taxon, origin)	Invader group: life history	Native species affected (*endemic)	Displacement/extinction	Suggested mechanism	Source
California, USA	*Ammophila arenaria* (Poaceae); Europe	Plant: grass	*Lupinus tidestromii* (endangered)	Population models derived from field data projected that 2 of 3 study populations will decline toward extinction under ambient levels of consumption	Apparent competition: native species experienced high levels of pre-dispersal seed consumption by the native rodent *Peromyscus maniculatus* from the proximity to the non-native grass *Ammophila arenaria*	Dangremond et al. (2010)
Alberta, Canada	*Bromus inermis, Poa pratensis* (Poaceae); Eurasia	Plant: grass	*Anemone patens*	Long-term persistence of *A. patens* in habitats dominated by non-native grasses is unlikely	Decreased survival and reduced population growth of *A. patens* among non-native grasses	Williams and Crone (2006)

California, USA	*Aporrectodea trapezoides* (Lumbricidae); Holarctis	Invertebrate: earthworm	*Argilophilus marmoratus*	Displacement of the native species only occurs in disturbed habitats	Higher relative growth rates of non-native *Aporrectodea* in high-productivity conditions	Winsome et al. (2006)
Mediterranean Sea	*Brachidontes pharaonis* (Mytilidae); Indian Ocean, Red Sea	Invertebrate: mollusk	*Mytilaster minimus*	Displacement following change of habitat; no extinction	Habitat degradation caused an increase in abundance of the invader, displacing the native through increased propagule pressure	Rilov et al. (2004)
North America	*Dreissena polymorpha* (Dreissenidae); Europe	Invertebrate: mollusk	Freshwater unionid bivalves	Of the historic 281 species, 19 are known to be extinct, 21 are thought to be extinct, 77 are endangered, 43 are threatened, and 72 are of special concern	Competition, substrate (habitat) and water quality alteration	Ricciardi et al. (1998)
Pacific islands	*Euglandina rosea* (Spiraxidae); North America	Invertebrate: mollusk	Endemic snails*	More than 100 endemic species are considered to be extinct	Predation of naive snails	Hadfield et al. (1993) and Régnier et al. (2009)

(continued)

Table 10.1 (continued)

Region	Non-native species (taxon, origin)	Invader group: life history	Native species affected (*endemic)	Displacement/extinction	Suggested mechanism	Source
California, USA; Mexico	*Cactoblastis cactorum* (Lepidoptera); South America	Invertebrate: insect	*Opuntia* spp.*	Some 80 *Opuntia* species endemic to Mexico and the USA are considered at risk; also cultivated and used wild species are considered vulnerable	Herbivory	Hoffman et al. (2000) and Stiling (2002)
Madeira	*Pieris rapae* (Lepidoptera); Europe	Invertebrate: insect	*Pieris brassicae* subsp. *wollastoni**	Introduction led to the extinction of the native subspecies	Disease transmission	Kenis et al. (2009)
Europe (UK, Belgium)	*Harmonia axyridis* (Coleoptera); Asia	Invertebrate: insect	*Adalia bipunctata*	Declines of 30–44 % over 5 years after the arrival of *H. axyridis* led to displacement of the native species	Direct predation and resource competition	Roy et al. (2012)
New Zealand	*Vespula vulgaris* and *V. germanica* (Hymenoptera); Europe	Invertebrate: insect	Birds*, insects	Several common and widespread bird species have had significant declines in their abundance of the last 30 years; attributable to the impacts of a number of introduced species, but especially wasps	Foraging behaviour of birds affected; Predation of caterpillars;	Kenis et al. (2009)

Christmas Islands, Australia	*Anoplolepis gracilipes* (Hymenoptera); Africa	Invertebrate: insect	*Gecarcoidea natalis**	The yellow crazy ant has killed millions of red crabs, approximately a third of the population, with subsequent invasional meltdown and significant declines of other species	Direct predation, nuisance and habitat modification by seed predation and removal	O'Dowd et al. (2003)
Lake Victoria, Africa (Kenya, Uganda, Tanzania)	*Lates niloticus* (Latidae); tropical Africa	Vertebrate: fish	Endemic cichlids	Extinction of 200 or more of the approximately 500 species radiation of endemic cichlid fishes (*Haplochromis* spp.)	Predation	Aloo (2003)
Spain	*Gambusia holbrooki* (Poeciliidae); North America	Vertebrate: fish	*Aphanius iberus* (cyprinodontid fish)	Extirpation of many populations	Mostly through predation on juveniles and possibly competition. Habitat alteration (e.g., salinity) mediates the interaction	Alcaraz and García-Berthou (2007)
Guam	*Boiga irregularis* (Colubridae); Australia	Vertebrate: reptile	Birds, bats, reptiles	Introduction led to the extinction of several bird species on Guam	Predation (incl. eggs); presence of alternate introduced prey	Fritts and Rodda (1998)

(continued)

Table 10.1 (continued)

Region	Non-native species (taxon, origin)	Invader group: life history	Native species affected (*endemic)	Displacement/extinction	Suggested mechanism	Source
Islands worldwide	*Felis catus* (Felidae)	Vertebrate: mammal	Birds, mammals, reptiles (48, 16 and 4 endemic, respectively)	Feral cats on islands are responsible for at least ~14 % of the modern bird, mammal, and reptile global extinctions and threaten ~8 % of critically endangered species in these groups	Predation; presence of introduced alternate prey (rodents and rabbits)	Medina et al. (2011)

Note that the overview is to illustrate the variety of mechanisms reported in various taxonomic groups rather than providing an exhaustive summary of known cases of extinctions and population declines caused by invasive species

Fig. 10.1 *Cinchona pubescens* invasion on the island of Santa Cruz, Galapagos. (Photograph by Heinke Jäger)

and the cover of most native species by at least 50 %, and of endemic herbs on average by 89 %, over 7 years (Fig. 10.1). However, the number of native, endemic, and non-native species in the study area remained constant: no plant species has been lost completely at the landscape scale (Jäger et al. 2009). Nevertheless, if the present 20 % cover of *C. pubescens* continues to grow, local extinctions are likely.

A range of studies suggest that, as with *C. pubescens*, plant invasions are generating situations where extinctions of native species are likely or inevitable given enough time, assuming that the trajectory of the invasion continues as it is. For example, meta-population models of Californian grasslands suggest that, even at low levels of invasion, the spread of European grasses may generate an extinction debt (Gilbert and Levine 2013). Although the time to extinction of the species that cannot persist with invasion in this system can be in terms of hundreds of years, these authors concluded that recent suggestions that plant invasions fail to drive native plant extinctions may be premature. In a similar vein, demographic models indicate that non-native grasses in Alberta, Canada, may cause slow declines in populations of the native *Anemone patens*, and that despite short-term coexistence, extinction risk in *Bromus inermis* grass patches is too high over a 50-year time period to make the survival of *A. patens* likely (Williams and Crone 2006).

The complexity of the interactions that may cause non-native plant species to drive out natives can be demonstrated in another coastal dune system in California.

Here, the endangered native plant *Lupinus tidestromii* experiences high levels of pre-dispersal seed consumption by the native rodent *Peromyscus maniculatus* as a result of the proximity of the non-native grass *Ammophila arenaria*. Population models projected that two of three study *Lupinus* populations will decline toward extinction under ambient levels of consumption (Dangremond et al. 2010). The phenomenon of consumer-mediated apparent competition posing a strong extinction threat to native plant species may be more frequent than realised if non-native plants can support large increases in consumer density, and hence consumption of native species and their seed. If this consumption occurs before seed dispersal, it can have strong population-level effects on native plants (see Dangremond et al. 2010 and references therein). Another mechanism that can eventually lead to population decline of a rare native species is hybridisation. For example, *Lantana depressa*, an endemic species in Florida, is hybridising with the non-native South American species, *Lantana camara*, and the hybrid offspring are competitively replacing the rare native (Schierenbeck 2011). Further evidence comes from Mauritius, where two plant species that were presumed extinct, several plant species that were critically endangered, and one endemic butterfly species, all recovered dramatically as a consequence of the removal of the non-native tree *Psidium cattleianum* (Baider and Florens 2011).

Our fears about the impacts of non-native plant species mainly derive from predictions, from explicit or implicit models, about the likely outcomes of on-going invasions and their potential to generate extinction debts (Gilbert and Levine 2013), rather than from direct observations of extinctions. However, the fact that no species extinctions have yet been caused solely by competition with non-native plants (Sax and Gaines 2008) is not an excuse for complacency. As with climate change, the predictions of models based on well-established processes cause significant concern and should not be dismissed without equally good evidence to the contrary.

10.2.3 Case Studies of Non-native Animals: Robust Evidence for Native Species Extinctions and Declines

In general, examples of native species population declines caused by animal invaders, both invertebrates and vertebrates, reflect clearer population impacts than are documented for plants, and often lead to local and global extinctions of native species. This trend is likely to result from the impacts of non-native animals often acting through predation or disease, both of which are strong and rapid processes compared to competitive displacement. Examples of non-native animal species that have driven native population declines and extinctions are given in Table 10.1.

Vertebrates: Mammals, Reptiles, and Fish Vertebrate invasions have been responsible for some of the most serious ecological catastrophes in history, which correspond with some groups, mammals in particular, having the most severe environmental impacts of all invading organisms. For example, a review of feral cats, *Felis catus*, on islands as drivers of native species extinctions (Medina et al. 2011) showed that impacts have been documented from at least 120 different islands on at least 175 vertebrate species (25 reptiles, 123 birds, and 27 mammals), many of which are listed as threatened by IUCN. Cat impacts were greatest on endemic species, particularly mammals, and were more severe if alternative non-native prey species, such as rodents and rabbits, were also introduced. Feral cats on islands are considered to be responsible for at least 33 global bird, mammal, and reptile extinctions recorded by the IUCN Red List (14 % of the 238 extinctions in total), and have contributed to the critically endangered status of 38 (8 %) of the 464 taxa within these groups. It is nonetheless important to keep in mind that these figures are conservative: the impact of cats on many, perhaps most, species has not been yet studied (Medina et al. 2011). The red fox, *Vulpes vulpes*, is another major predator responsible for species extinctions. Together with cats it is thought to have contributed to the disappearance of all but 2 of the 22 completely extinct marsupials and rodents in Australia.

A classic example of non-native mammal species driving native species to extinction is given by the avifauna of the New Zealand archipelago (Holdaway 1999). New Zealand had no native terrestrial mammal predators before around 800 years ago and the arrival of the Maori, who brought with them the Pacific rat, *Rattus exulans*. A wave of extinctions in the native avifauna followed this colonisation, with the species disappearing having characteristics that either made them attractive to human hunters (flightless, large-bodied species) or susceptible to Pacific rat predation (small-bodied, ground-dwelling, and ground-nesting species laying small eggs). A subsequent extinction wave followed the arrival of Europeans in the eighteenth century. They introduced additional non-native mammals, such as cats, stoats (*Mustela erminea*), and black and brown rats (*R. rattus* and *R. norvegicus*), which preyed upon species that had thus far survived by being too large to be susceptible to Pacific rats and too small to be of interest of humans (Holdaway 1999). A specific example of these impacts concerns the black rats that reached Big South Cape Island around 1964 (Bell 1978, cited in Courchamp et al. 2003). This island was, up to that point, free of non-native predatory mammals and was home to the last viable populations of four endemic vertebrate species that had formerly been widespread across New Zealand (South Island snipe, *Coenocorypha iredalei*; South Island saddleback, *Philesturnus carunculatus*; bush wren, *Xenicus longipes*; greater short-tailed bat, *Mystacina robusta*). Once local conservationists realised that rats had reached the island, attempts were made to catch and translocate individuals of these four species to other islands. Some of these translocation programs were, however, unsuccessful, and three of these species are now globally extinct as a result.

These repeated examples of the temporal coincidence between non-native mammal species arrival and the extinction of bird species with traits that make them susceptible to predation strongly suggest cause and effect (Holdaway 1999). Further examples of massive extinction events following vertebrate biological invasions concern a fish and a snake. The former refers to the invasion of Lake Victoria in Africa by the Nile perch, *Lates niloticus*, in the 1950s, which was followed by the extinction or near-extinction of several hundred endemic cichlid fishes. However, fishery overexploitation, eutrophication, and invasion by the water hyacinth, *Eichhornia crassipes*, have also been related to the decline of native fishes (Aloo 2003). No such ambiguity surrounds the other example, which relates to the invasion of the brown tree snake, *Boiga irregularis,* following its accidental introduction to Guam in the 1950s. This invasion induced a cascade of extinctions that may be unprecedented in terms of taxonomic scope and severity. The most affected taxa were birds, bats, and reptiles, and by 1990, Guam harboured only three native vertebrates, all of which were small lizards. A few other species persisted on small, offshore islands not reached by the snake. An important factor in this invasion was the presence of alternate introduced prey, such as the curious skink, rats, and mice, that contributed to maintaining the populations of the invader at high levels while it was driving the native prey species to extinction (Fritts and Rodda 1998).

Invertebrates: Earthworms, Mollusks and Insects As for non-native plants, the presence of non-native invertebrates often goes hand in hand with other anthropogenic impacts, making it hard to draw clear conclusions about the effects of non-natives in suppressing native species populations. For example, the displacement of native earthworms in California by the non-native Holarctic earthworm, *Aporrectodea trapezoides*, only happens in disturbed habitats (Didham et al. 2007). Similarly, habitat change and sedimentation in the Mediterranean Sea allowed an increase in the abundance of a non-native mollusk *Brachidontes pharaonis*, and local displacement, without extinction, of a native species (Rilov et al. 2004). Even the devastating impact of the invasion of *Dreissena polymorpha* in North America that resulted in the presumed extinction of around 40 native freshwater unionid bivalves cannot be unequivocally attributed to this invasion alone but to habitat destruction and deterioration as well (Ricciardi et al. 1998).

Biocontrol agents have been deliberately released with unintended consequences for native species. Among mollusks the predatory rosy wolfsnail, *Euglandina rosea*, was introduced as a biocontrol agent against the giant African landsnail, *Achatina fulica*, to many Pacific islands, and it is estimated one-third of native mollusk extinctions on oceanic islands may have been caused by the introduction of *E. rosea* (Régnier et al. 2009). Similarly, the cactus moth, *Cactoblastis cactorum*, native to South America and a successful biocontrol agent against *Opuntia* in many places around the world, has been introduced accidentally to southeast USA where it is a serious threat to endemic *Opuntia* species (Myers and Cory 2017). There is also convincing evidence for the substantial decline of native ladybird species as a consequence of the introduction of the harlequin ladybird, *Harmonia axyridis*, in Europe (Myers and Cory 2017), but again, there is no evidence of extinctions as yet (Fig. 10.2).

Examples of insects driving population declines include the North American non-native wasp, *Vespula pensylvanica*, that by direct predation and exploitative competition make several Hawaiian native bee and wasp species, including endemics, avoid floral resources occupied by the invader and become absent from areas near its colonies. The European *Vespula germanica* and *V. vulgaris*, introduced to

Fig. 10.2 Introduced *Harmonia axyridis* is displacing native ladybird species in Europe. (Photograph by Wolfgang Rabitsch)

New Zealand, prey on other arthropods, specifically butterflies, but also negatively affect endemic bird foraging behaviour (Table 10.1). Both cases point to the vulnerability of native island biota to ecological disruption caused by continental species. Ants provide multiple lines of evidence for competitive displacements of native species on all continents as well as many islands (Holway et al. 2002). The yellow crazy ant, *Anoplolepis gracilipes*, has decimated the population of native red crab on Christmas Island (O'Dowd et al. 2003). The Argentine ant, *Linepithema humile*; the red imported fire ant, *Solenopsis invicta*; the bigheaded ant, *Pheidole megacephala;* and several other non-native ant species have displaced native ant species and reduced diversity almost everywhere they have become established, yet no extinction of native species has been reported so far. The extinction of the endemic Madeiran large white butterfly, *Pieris brassicae* subsp. *wollastoni*, is considered to have been caused by the introduction of, and disease transmission by, the related *Pieris rapae* (Kenis et al. 2009).

10.3 What Makes a Native Species Vulnerable to Population Decline and Extinction Resulting from Invasion?

Several principles have been put forward to explain differences in the vulnerability of particular taxonomic groups to population declines or extinctions caused by invasions, illustrated in these examples.

(i) Non-native predators and pathogens are far more likely than non-native competitors to cause the extinction of native species (Gurevitch and Padilla 2004). (ii) The most vulnerable species are island endemics; among hypotheses to account for the severity of extinction events on islands is the lack of coevolution between introduced predator and prey (Duncan et al. 2013). (iii) Presence of alternative non-native prey of the non-native predator increases the probability that it will drive the native prey to extinction (Fritts and Rodda 1998). The case studies summarised in

Table 10.1 further illustrate that island-like situations, be they oceanic islands or freshwater lakes, contribute to severe impacts because the affected native taxa have nowhere to escape. Islands with refuges tend to suffer lower levels of loss (Duncan et al. 2013).

One principal difference among plants and insects on one hand, and vertebrates on the other, related to the opportunity to escape from the immediate impact of the invader, is the presence of dormant stages in the former, such as seeds or pupae, which make it possible to escape not only in space but also in time, by waiting for more favourable conditions. Another explanation for the obviously less severe impacts, in terms of extinctions, on plants compared to vertebrates was suggested by Sax and Gaines (2008). For birds on islands, these authors suggest that the colonization-based saturation point has been reached, meaning that new species cannot be added unless existing species are removed. For plants, there is no evidence of extinction-based saturation on islands; this assumption is supported by the great numbers of plants that have become naturalized on islands worldwide (Sax and Gaines 2008) although relatively few native species have become extinct. Nevertheless, there is no robust evidence for colonization-based saturation in birds either, and we think that other explanations for the different levels of extinction between birds and plants on islands (e.g., the different interaction mechanisms at play) are more likely.

10.4 Conclusions

This review provides robust evidence accumulated over the past decade that non-native species cause local and global extinctions. Nevertheless, the impacts are not felt equally by all taxa, and direct evidence of native species extinctions as the result of invasion is still largely lacking for plants, and to some extent also for insects. We still need better data to allow us to separate unequivocally the cases of proven direct effects of invading non-native species on population declines and extinctions of native taxa from those where both the invading non-native and affected native species are passengers of the environmental change, such as habitat degradation (Gurevitch and Padilla 2004). Although many (if not most) extinctions can be attributed to multiple causes, among which non-native species are one of the contributing factors (and sometimes might be “the final nail in the coffin”), substantial datasets coincide in showing that non-native species do have an important role in these processes (Bellard et al. 2016).

One strong signal that has been already noticed by Gurevitch and Padilla (2004) is that a few non-native species have been known to cause a disproportionately large share of documented extinctions (Table 10.1). Prominent examples include cats, the brown tree snake, a few widespread rat species, predatory snails and fishes, and possibly also annual Mediterranean grasses. In general, however, non-native plant and insect impacts are expressed in terms of local displacement of native species and community changes, rather than in species extinctions. Interestingly, these 'superinvaders' that drive native biota to extinction comprise relatively few species (compared to the large number of introduced species worldwide) but recruit from diverse functional groups. Our review nevertheless indicates that despite some scepticism about the importance of non-native species for extinctions (Gurevitch and Padilla 2004; Sax and Gaines 2008), evidence has accumulated that makes it impossible to dismiss the impacts of non-native species, and in particular vertebrate animals, as drivers of native population declines and extinctions.

Although much still needs to be learned about the functionalities and interdependencies between biodiversity in all its expressions, it is evident that the increasing loss of native species can have cascading effects on interspecific species interactions and thus on regulating services. Because non-native species contribute to this loss, any attempts to reduce their impact means safeguarding ecosystem services provided for future generations.

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Chapter 11
Infections and Diseases in Wildlife by Non-native Organisms

Serge Morand

Abstract Parasites and diseases can have important effects on both non-native and native species. In this chapter, several mechanisms for these processes are discussed, including the parasite immunocompetence advantage; novel weapons from spill-over of co-introduced parasites; parasite spill-back of native parasites to introduced species; and dilution effects that influence the success of an invader and the impacts on the invaded region. Trophic cascades can also have dramatic consequences of disease-related invasions, in which the invasion of parasites may ultimately lead to the extinction of native species through the disruption of biotic interactions in the invaded community. As there is no consensus on the service of biodiversity and conservation as a protection against diseases, the need to conduct research on the impacts of diseases associated with biological invasions on ecosystem regulating services is emphasised. Moreover, further investigation is prompted into better assessments of the ecological causes influencing disease spread in wildlife associated with invasive species, as these developments may ultimately affect human health.

Keywords Biotic resistance • Dilution effect • Disease regulation • Immunocompetence advantage • Novel weapon • One World One Health • Parasite release • Spill-back • Spill-over

11.1 Introduction

The literature on ecosystem services is considerable, and growing, but studies specifically devoted to infectious disease control are few and mostly theoretical in their approach. Even the indicators concerning the regulating ecosystem services for disease spread, either developed or validated, are few in number, which is likely

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explained by the lack of scientific consensus on the links between biodiversity loss and health risks in relationship to infectious diseases (Lafferty and Wood 2013).

Parasitism affects individual hosts, populations, communities, and even ecosystems. As a consequence, parasites can have an important role in biological invasions, controlling the success of introduced host species (Møller and Cassey 2004; Dunn et al. 2012) as well as their impacts on native hosts and ecosystems (Dunn et al. 2012). For example, spill-over of introduced parasites and spill-back of native parasites transmitted by introduced hosts appear to have important consequences for ecological systems, wildlife, domestic species, and humans that pose new health risks (Hatcher et al. 2012).

According to Kolar and Lodge (2001), the invasion process can be described in three main steps: introduction, initial establishment, and spread. The first step is associated with the dispersal ability of the species and its dependence on human activities. The second step, the establishment, depends on the interaction with the local environment and biota. The last step, spread or population growth, depends on the biological characteristics of invasive species and the effects of species interactions, such as competition, predation, and parasitism, as well as the environment. Indeed, biological invasions are often compared to disease epidemics as these processes share analogous features, such as the chance of establishment, the initial population growth, and the impacts in the new range, specifically on the host population. Moreover, the species diversity of parasites, that is, polyparasitism or multi-infection, in either native or invasive hosts, has an important part at each step of the invasion.

The aim of this chapter is to review the main hypotheses on the effects of parasitism and disease on the outcome of biological invasions: (1) parasite release (i.e., the enemy release hypothesis); (2) immunocompetence advantage; (3) the novel weapons hypothesis, from the spill-over of co-introduced parasites; (4) the spill-back of native parasites to introduced species; (5) the dilution effect hypothesis, the result of the buffering influence of biodiversity on parasite spread; and (6) resource allocation of non-native invaders, all of which may affect ecosystem functioning through trophic cascades (Fig. 11.1).

These hypotheses are not mutually exclusive and can interact or oppose one another. Indeed, in the invasion process, hosts harbouring a high diversity of parasites in their native locations have a fourfold advantage in relationship to the previous hypotheses. First, parasites are often “lost” during the invasion process, and introduced species may be released from their demographic control. Second, introduced hosts may have evolved strong immune defences in their natural range, which confer a high capacity to control parasites that they may acquire by spill-back in the introduced environment. Third, native hosts may have also evolved strong immune defences, which confer resistance against the spill-over of introduced parasites. Fourth, introduced parasites may have been introduced along with the invader and spill-over to native hosts. Fifth, introduced species, in the absence of parasites in the invaded localities, may reallocate energetic resources from unnecessary costly defences into fitness and growth, leading ultimately to establish and spread by increased competitive ability, as proposed by Blossey and Notzold (1995).

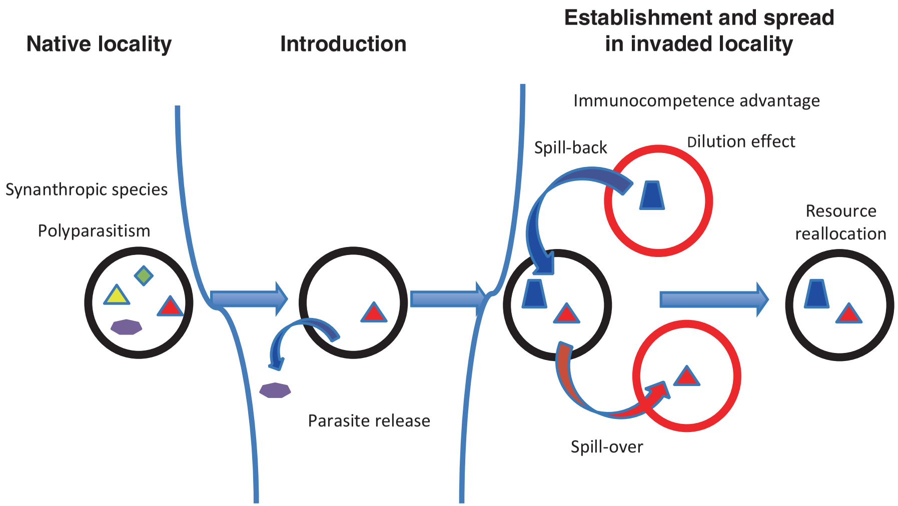

Fig. 11.1 Parasite-related traits in the native locality and mechanisms involved in the invasion of the introduced locality. The introduction is associated with the polyparasitism of the host species, the dispersal ability of the parasite, its dependence on human activities (e.g., synanthropy), and its ability to release parasites. The main mechanisms involved in the establishment and spread in the invaded locality are immunocompetence advantage, to cope with spill-back of parasites from the invaded locality; spill-over of co-introduced parasites; and dilution effects reducing spill-back of parasites from hosts of the invaded locality. *Large circles* indicate host species; *small figures* indicate parasites

11.2 Parasite Release Hypothesis

The parasite release hypothesis, originally named the enemy release hypothesis, was proposed as an ecological mechanism to explain the success of introduced species when invading a new environment. Introduced species could gain a competitive advantage over local species if they are differentially released from control by parasites (Dunn et al. 2012). Studies, mostly on plants or invertebrates, have shown that the parasites of an introduced species are either left in its native area, are lost, or cannot establish in the invaded habitat (Marzal et al. 2011; Dunn et al. 2012). One example concerns the invasive Polynesian rat, *Rattus exulans* (Roberts 1991). When investigating the parasite communities of this species in Southeast Asia and the Pacific islands, one can show that there is a decrease in parasite species richness from insular Southeast Asia (its putative area of origin) compared to mainland Southeast Asia and the Pacific Islands (invaded areas). Similarly, López-Darias et al. (2008) showed a reduced parasite diversity in the invasive Barbary ground squirrel, *Atlantoxerus getulus,* in the Canary Islands compared to North African native populations. Not only invasive mammals on islands showed reduced parasite communities. For example, Bordes et al. (2007) investigated the helminth communities of the introduced Iberian hare, *Lepus granatensis*, in southern France, showing that the hare harboured a reduced community of parasites relative to the helminth communities in its native habitat in Spain.

Interestingly, the parasite release hypothesis explains factors associated with co-invader parasites. Hence, associated introduced parasite species may not establish if they do not encounter a suitable host in the invaded localities. For example, Goüy de Bellocq et al. (2002) investigated the structure of helminth communities of rodents in the Mediterranean area and showed that there was a significant decrease of helminth species richness in the invasive *Rattus rattus* in relationship to geographical distances from invaded Mediterranean islands to the mainland area. Moreover, direct-transmitted helminths were the best co-invaders, a parasite life trait that appears related to invasion capacity, compared to helminths with a complex life cycle that requires intermediate hosts.

11.3 Immunocompetence Advantage Hypothesis

Among the physiological traits that favour the establishment and spread of invasive species in new localities are those that help at coping with parasitism. The immunocompetence advantage hypothesis posits that hosts, having evolved strong immune defences, are then prime candidates for successful invasion (Møller and Cassey 2004). The immunocompetence advantage hypothesis echoes the increased competitive abilities hypothesis (Blossey and Notzol 1995) wherein the lack of the need for immune defence allows reallocation of resources toward growth and reproduction.

This hypothesis requires testing from an immunological point of view (e.g., immunogenetics, investigating structure and function of genes, and immunoecology, investigating adaptive and innate immune responses in an ecological context) with regard to the invasive species in its native distribution and in the invaded localities, together with its sympatric congeners with which the chances of sharing parasites are high. Very few immunoecological or immunogenetics studies have been conducted in this sense (White and Perkins 2012).

Møller and Cassey (2004) have investigated the relationship between the T-cell-mediated immune response in birds and their establishment success in non-native invaded areas. They showed that species with stronger responses were more successful in becoming established. As high investment in immunocompetence in hosts is related to parasite loads and impacts, it confers high resistance against spill-back of parasites in the invaded environment.

Immunogenetics studies usually find a decrease in the diversity of immune genes in invasive populations. However, the diversity per se in immune genes does not reflect the success of the invasion success, which necessitates investigation of the functional relevance of the immune genes to cope with the local parasites (Monzon-Argüello et al. 2013). Mismatch of functional immune genes to local parasites may lead to maladaptive and costly immune responses. Few studies have investigated the immunocompetence advantage in mammals, and so far significant differences in immunocompetence among native and invasive insular populations have not been found (Morand et al. 2010).

11.4 Spill-over and Novel Weapons Hypothesis

The novel weapons hypothesis suggests that introduced species may arrive in a new location with biochemical or biological novelties that differentially impact native competitors to a greater degree. One example of this is parasite spill-over, in which a host co-introduces a novel parasite that may “jump” into local native hosts (Strauss et al. 2012). Several studies have shown co-introduced pathogens that have pushed native host populations to extinction (Table 11.1).

One recent example of spill-over is the introduction of the poxvirus to England by the North American grey squirrel, *Sciurus caolinensis*. The disease caused by the virus has led to the local extirpation of the highly susceptible native red squirrel, *Sciurus vulgaris,* presumably enabling the rapid spread of its competitor, the grey squirrel (Tompkins et al. 2003). An historical example is the introduction, by black rats, of the bacterium that causes plague, *Yersinia pestis*. In the mid-fourteenth century, one third of the European human population died of the plague, for which black rats were assumed to be the source. Another pandemic of plague started in China and spread around the world by ships carrying rats infested by *Y. pestis* and imported into San Francisco in 1899. Introduced strains of *Y. pestis* spilled over to the local rodent communities with some devastating consequences, such as the decimation of highly susceptible black-prairie dog, *Cynomys ludovicianus*, populations

Table 11.1 Some examples of host–parasite systems with consequences on parasites and diseases following invasion and the likely mechanisms involved

Mechanism	Consequence	Host–parasite system	Region	Reference
Parasite release	Initial establishment and host spread	Invasive *Rattus rattus*/helminths	Mediterranean mainland and islands	Goüy de Bellocq et al. (2002)
	Initial establishment and host spread	Invasive *Rattus exulans*/helminths	New Zealand and Polynesian islands	Roberts (1991)
	Initial establishment and host spread	Invasive *Atlantoxerus getulus*/ helminths	North Africa and Canary Islands	López-Darias et al. (2008)
	Initial establishment and host spread	Invasive *Lepus granatensis*/helminths	Southern France and Spain	Bordes et al. (2007)
Immunocompetence advantage	Initial host establishment and ability to cope with local parasite	Invasive rodents/helminths	Mediterranean mainland and islands	Morand et al. (2010)
Parasite spill-over and novel weapons	Extinction of native host	Invasive *Sciurus carolinensis* to native *Sciurus vulgaris*/squirrel poxvirus	UK	Tompkins et al. (2003)
	Decline of native hosts	Invasive *Rattus rattus* to humans and local rodents/Yersina pestis (plague)	USA	Cully et al. (2010)
	Extinction of native hosts	Invasive *Rattus rattus* to native *Rattus macleari*/*Trypanosoma lewisi* (protist)	Christmas island	Wyatt et al. (2008)
	Unknown	Invasive *Rattus rattus* to native *Peromyscus maniculatus*/*Trichuris muris* (helminth)	Islands in USA	Smith and Carpenter (2006)
	Extinction of native hosts	Invasive *Culex quinquefasciatus* to native birds/*Plasmodium relictum* (protist)	Hawaii	van Riper et al. (2002)
	Decline of native hosts	*West Nile* virus to native birds	USA	Ladeau et al. (2007)
	Extinction of native hosts	Invasive *Rana catesbeiana* to native frogs/*Batrachochytrium dendrobatidis* (fungus)	Worldwide	references in Hatcher et al. (2012)

Parasite spill-back	Amplification effect	Invasive *Rattus exulans* to humans/*Orientia tsutsugumishi* (bacteria)	Taiwan	Kuo et al. 2011
Dilution effect	Reducing transmission of local parasite	Invasive *Clethrionomys glareolus* to local rodents/*Bartonella birtlesii*, *Bartonella taylorii* (bacteria)	UK	Telfer et al. (2005)
Trophic cascade	Extinction of a native butterfly	Invasive *Oryctolagus cuniculus*/*Myxoma* virus	UK	Manchester and Bullock (2000)
	Decline of native hosts, reduction of grasslands, decline of predators, extinction of rabies and canine distemper virus	*Bos indicus* to native antilopes and local livestock/*rinderpest* virus	Africa	Dobson (1995)

(Cully et al. 2010). Similarly, Wyatt et al. (2008) provided molecular evidence for trypanosome infection by *Trypanosoma lewisi* in endemic rats, *Rattus macleari*, on Christmas Island after the introduction of black rats. By using museum tissue collections, the authors showed the lack of trypanosome infection in endemic rats collected before the introduction of black rats together with fleas and the parasitic protist.

Although the first major extinction of Hawaiian birds occurred following the arrival of the first Polynesians and their animals, and in the early European exploration and colonization, the extinction of some Hawaiian bird species has been attributed to avian malaria, *Plasmodium relictum* (van Riper et al. 2002). The transmission of this protozoan is related to introduction of the mosquito *Culex quinquefasciatus* in 1826. Endemic birds were then exposed to the parasite, either co-introduced with domestic birds or harboured by migratory birds passing through Hawaii (van Riper et al. 2002). Endemic survivor birds now live above 1300 m altitude, at which the vector cannot establish because temperatures are too low for its survival.

The West Nile virus started to invade North America a decade ago, resulting in around 200 human deaths every year and a significant decrease in abundance for some bird species (Ladeau et al. 2007). The virus originated in bird populations in Africa, and is commonly found also in Middle East, Europe, and Western Asia. The invasion started during the summer of 1999 with an outbreak of human encephalitis caused by West Nile virus in New York City, where, at the same time, unusual high mortality was detected among the birds at the Bronx Zoo. Following this initial event, the virus spread in North America among resident birds, leading to a large decline of some populations (Ladeau et al. 2007).

The fungus *Batrachochytrium dendrobatidis* emerged as a global threat to amphibians in association with several environmental stressors, such as habitat destruction and climate change. The invasive American bullfrog, *Rana catesbeiana*, is known to spread the fungus to native amphibian species. The fungus is of low virulence to the invader, but causes high mortality in native species (Hatcher et al. 2012). A lower virulence of the fungus in the invasive frog is also in accordance with the immunocompetence advantage hypothesis, although the precise mechanism of virulence is not fully known.

Smith and Carpenter (2006) also noted the introduction of a nematode likely introduced by black rats, *Rattus rattus*, to native deer mice, *Peromyscus maniculatus*, on the California Channel Islands. The consequences of this spill-over on the decline of the native deer mice are still uncertain. However, and although the black rats were finally eradicated, the introduced nematode continued to thrive in the native deer mice. A co-introduced parasite may then have the potential to remain following a spill-over in a native population even after its non-native host was extirpated.

11.5 Parasite Spill-back Hypothesis

Following their introduction, abundant introduced species can also serve as hosts to amplify transmission of local native parasites, which then spill-back to native hosts. For example, one recent study concerned the Pacific rat, *Rattus exulans*, originating from insular Southeast Asia, which recently invaded some localities in Taiwan. Kuo et al. (2011) demonstrated that this invasion contributed to the local spread of scrub typhus by spill-back of the bacterial agent *Orientia tsutsugumishi* in the invasive competent rodent. As the bacteria is transmitted by chigger mites, the spill-back necessitates that the invasive Pacific rat should be parasitized by local chigger mites that carried *O. tsutsugumishi* gained from local rodents. Indeed, such indirect transmission of local parasites is likely to occur as the chigger mites show low specificity toward rodent species.

11.6 Dilution Effect Hypothesis

The pioneering work of Elton on the “disease diversity hypothesis” in plants has found recent echoes with the “dilution effect hypothesis” in animals, which suggests that host species diversity may act as a potential buffer to parasite invasion, similar to the biotic resistance in biological invasions. The dilution effect occurs when the addition of one or more less competent host species to a host community contributes to “wasted transmissions,” which reduces parasite transmission despite the presence of highly competent host species. This situation may occur where a local parasite is locally adapted to its native host. Then, the transmission to a potentially less suitable non-native host may create a kind of dilution effect because of the loss of infective stages of the parasite in the less competent host. This dilution lowers the prevalence of infection in the native host.

The extent to which diversity can regulate infectious disease is hotly debated (Lafferty and Wood 2013), with most studies focusing on human diseases and plant diseases, but a few concern wildlife diseases that are non-zoonotic. For example, Telfer et al. (2005) observed a decline in the prevalence of two intracellular bacteria, *Bartonella birtlesii* and *Bartonella taylorii*, in populations of the wood mouse *Apodemus sylvaticus,* with the increase in density of the invading bank vole *Clethrionomys glareolus*. As a consequence, the invasive bank vole reduced the impact of infection vectored by fleas on wood mice.

11.7 Trophic Cascades

Trophic cascades occur when removing predators alters the functioning of an entire food web through the changes in the lower trophic levels. A classic example of this is the introduction of rabbits in Australia that resulted in a tremendous population explosion, with considerable impacts on Australian grassland ecosystems. Because of the lack of predators and pathogens for rabbits found in Australia, the idea of biological control of the rabbit by the introduction of myxomatosis virus, originated from South America, was proposed in 1950 by the Australian authorities. The rabbit population, estimated at more than 600 million before the introduction of the virus, dropped to 100 million in 2 years. Faced with such success, the myxomatosis virus was also introduced in Europe a few years later. Similar drastic reductions in rabbit populations were observed in Europe, but with unintended consequences. For example, in Britain, the introduction of the virus led to the extinction of a butterfly, *Maculinea arion*. This unpredictable extinction was related to the great specialisation of this butterfly, which has a symbiotic dependence with ants (Manchester and Bullock 2000). Rabbit populations in strong decline in response to the impact of the virus were no longer able to regulate the plant species they usually ate. The modification of plant communities and plant dynamics altered the competitive balance between the plant species eaten by rabbits and other plant species used by ants, leading to a reduced ant workforce.

Another example is rinderpest virus, which appeared in the Horn of Africa during the 1890s, in connection with the introduction of infected cattle from India. Rinderpest virus, a morbillivirus related to the measles and canine distemper viruses, caused between 80 % and 90 % mortality in wild ungulates in Africa, especially in large parks such as the Serengeti (Tanzania), with unrecorded ecological and social consequences (Dobson 1995). The outbreak lowered the ungulate populations well below the ecosystem carrying capacity, which affected predator populations and vegetation dynamics. The decline of the ungulate population also led to the decline of predators, with the consequence that rabies and distemper disappeared in wild carnivores. The declining transmission of both diseases was below the threshold transmission to sustain them in the wild populations. Domestic ungulates were not spared. Local livestock, the main resource of breeder pastoral communities, was also dramatically affected. Rinderpest occasioned a terrible famine in the Nuer that changed their social organisation. The disease remained endemic for decades until the use of vaccination achieved control and then eradication of this plague in the 1950s. The eradication of the rinderpest led the numbers of wildebeest to increase from 300,000 in 1960 to more than 1 million in the years 1980–2000. However, these changes were not without significant consequences for the functioning of the ecosystem, as the recovery of ungulate populations affected the vegetation dynamics. Bush fires diminished in numbers and intensities in relationship to the decline of plant biomass. A new equilibrium has emerged, but the current geographic distributions of many species of wild antelopes are still reflecting the effects of this introduced disease. Here, the accidental introduction of rinderpest with Indian cattle significantly affected the socioecosystem functioning of African savannahs.

11.8 Infectious Diseases: Valuation and Policies

Although ecosystem services related to biological invasions are able to estimate costs of biological invasions, disease regulation are mostly evaluated by the costs of inaction, such as increased human morbidity, increased costs associated with crop damage, or increased costs associated with biodiversity loss. Moreover, most studies on regulating infectious diseases concern human or livestock diseases and few wildlife diseases (see Delahay et al. 2009). For example, Valle and Clark (2013) emphasized that reducing the deforestation rate, and improving conservation, may ultimately lead to an increased malaria burden among local people with increased mortality and associated health costs.

Various international forums and organisations aim to provide recommendations and policies to regulate diseases affecting food provision and health: the Food and Agriculture Organisation (FAO), the World Organisation for Animal Health (OIE), and the World Health Organisation (WHO). These institutions have tried to work better together. The international initiative “One World One Health” according to the “Manhattan Principles” promoted by the non-governmental organisation, the World Conservation Society (www.oneworldonehealth.org), attempts to connect the objectives of preserving biodiversity with human and animal health. “One World One Health” aims to encourage cross-sectoral collaborations to better detect and respond more effectively to the emergence of infectious diseases at the animal–human–environment interface. The dialogue between ecological sciences and social sciences and stakeholders from different sectors is of paramount importance to understand and achieve disease regulations that affect both wildlife and humans.

11.9 Conclusions

Although data on the role of parasites in invasions continue to emerge, there is still a considerable lack of knowledge on how these processes affect ecosystem services in general. There are several hypotheses, supported by empirical data, related to how parasites influence invasion. Contrasting these hypotheses, and examining potential interactions between them, may provide clues for further research.

Clearly, the risks of disease introduction in invaded localities, or outbreaks of native diseases, are dependent on the types of introduced and native pathogens, their ability to spill-over or spill-back, and the features of invaded localities. Thus, the following research areas in particular warrant further investigation:

First, the importance of synanthropic species (i.e., species associated with humans) as potential invaders. In response to the high introduction opportunities associated with their behaviour and ecology, synanthropic species often show high parasite diversity in their native habitats, conferring significant advantages for invasion. Synanthropic invasive species might show high immunocompetence in their native localities together with high diversity of parasites, that is, a high potential of parasite release and high immunocompetence advantage. Comparative immunogenomics and immunoecology should provide clues of the resistance of invasive species to native parasites and against spill-back parasites compared to native species. Moreover, a better comprehension of the immunogenetics and immune responses of invasive species may help to develop biocontrol strategy by spill-back parasites.

Second, the role of biodiversity in disease spread deserves more attention. According to the dilution effect, the risk of disease spread might be higher in invaded species-poor communities such as islands (Derne et al. 2011). However, conflicting results have emerged in the recent literature. Experimental research manipulating communities, such as the work done by Suzán et al. (2009) on islands for hantavirus, is needed to avoid the confounding effects that are likely to occur in observational studies.

Third, the importance of human-dominated habitats in disease spread is of major concern. The risk of disease spread is expected to be higher in human-dominated habitats: this is a corollary prediction of the two preceding points, but rather than looking at species richness or diversity in the invaded communities, we should focus on the habitat structure and connectivity that may favour invasion and disease transmission to native hosts. This research would highlight how disturbance at the local and regional scale can influence disease outbreaks and their spread through the landscape.

The consequences of disease introductions or disease outbreak in the invaded environment may have dramatic effects on local species extinctions, which may in turn affect ecosystem functioning (as observed for myxomatosis or rinderpest). Introduced diseases, directly or through invasive species, are of major concern in conservation biology, but also for public health or veterinary health. Indeed, ongoing global changes and global trades will escalate new threats. For instance, among the 64 invasive bird species reported to cause impacts in Europe, 10 species cause health impacts (Shirley and Kark 2009). Thus, there is an urgent need to link basic and applied research to wildlife conservation and human health, and to consider the whole complexity of interactions between introduced diseases and parasites and non-native organisms, from physiology (immunology) to population and epidemiological dynamics in human-dominated ecosystems.

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Chapter 12
Biological Control Agents: Invasive Species or Valuable Solutions?

Judith H. Myers and Jenny S. Cory

Abstract To a large degree, the most serious insect and weed pests around the world are non-native, invasive species. Classical biological control, the introduction of natural enemies of invasive species to limit their populations, is a possible mechanism for alleviating the impacts of non-native pests. Whether introducing more non-native species in this way is a good approach depends on the positive and negative impacts of the potential control agents relative to the economic and environmental damage caused by the pests. Many classical biological control programs are deemed to be successful and contribute positively to ecosystem services by reducing the need for insecticides and herbicides as well increasing agricultural production, improving soil moisture conditions, and increasing native biodiversity. Recently, non-target impacts of some species of biological control agents have received considerable attention, which has impeded new classical biological control initiatives. However, analyses of the effectiveness of pre-release screening of agents shows that biological control has been very effective, particularly for weed control programs. Only 1–2 % of released agents have caused some damage to non-target species, and few have been shown to become invasive in the sense of being introduced, established, and having negative impacts in the new ecosystem. Clearly, generalist predators and parasitoids with multiple generations a year and multiple hosts should not be introduced because the potential for non-target impacts will be high. Host plant testing and specificity are important for choosing weed control agents, but must be viewed in the ecological context of species distributions and phenologies. However, the costs of lost opportunities from overly restrictive regulations must also be considered in evaluations of potential future classical biological control programs.

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12.1 Introduction

Classical biological control, based on the introduction of natural enemies, is often the only long-term solution for reducing the impacts of invasive, non-native pests. Despite the complex nature of selecting agents for their effectiveness on target pests and potential influences on other aspects of the community in which the target species is embedded, classical biological control of plants and animals has been remarkably successful. Of programs against non-native insects, 15–62 % have been reported to be successful (De Clercq et al. 2011). Estimates of successful biological control of weed programs vary: New Zealand, 83 % (Fowler 2000) or 24 % (Suckling 2013); Mauritius, 80 %; South Africa, 61 %; Australia, 51 %; and Hawaii, 50 % (Culliney 2005). Fowler (2000) suggested that success could be even higher if more resources were devoted to biological control programs. In the simplest interpretation, success is measured as reduced density of the target species, but the impacts of reduced densities on ecosystem services can involve increased forage or agricultural production, reduced insecticide or herbicide use, reduced competition with native organisms, increased biodiversity, improved stream flow, and increased economic value of land (Van Driesche et al. 2010). Suckling and Sforza (2014) reported the benefits of biological weed control to be as great as US$180 M a year in the USA, with similar positive environmental and economic evaluations in other countries. Benefit-to-cost ratios (benefit:cost units) can be high for successful classical biological control programs of weeds and insects. For example, van Wilgen et al. (2004) suggest a ratio of 740:1 for the cassava mealybug, *Phenacoccus manihoti*, and 4333:1 for the golden wattle, *Acacia pycnanthya*, in Africa. General figures for weed biocontrol range from 2 to 4000:1 (Culliney 2005). These high values are partially influenced by the assumption that biological control is a long-lasting solution.

Classical biological control programs for insects and weeds have involved the introduction of thousands of species of insect predators, parasitoids, and herbivores, as well as fungi, viruses, nematodes and bacteria. For each classical biological control program, several species are usually introduced, with an average of three per program for weeds and two per program for insects (Denoth et al. 2002). Thus, for every introduced, non-native target pest, the number of new species added to the community is increased several times over. Here, we consider how the general success of classical biological control relates to other potential impacts of these programs. What is the balance between positive and negative ecosystem services of introduced biological control agents?

12.2 Do Biological Control Agents Become Invasive?

The aims of classical biological control are positive, but do any of the species introduced become invasive? That is, do they establish, spread, and have negative impacts in the new environment? It is interesting to compare the establishment of biological control agents to patterns observed for introduced species in general for which the "Tens Rule" has been proposed: 10 % of introduced species become established and 10 % of those become invasive (Williamson and Fitter 1996). For biological control, establishment of introduced agents is higher: 60 % for agents on weeds and 52 % for those on insects (Denoth et al. 2002). These figures are not surprising as large numbers of agents are released in biological control programs to habitats well matched for the species. As we discuss next, however, if negative impacts refer to non-target effects, only about 1–2 % of established biological control agents result in negative impacts (Hajek et al. 2007; Van Driesche et al. 2010; Suckling and Sfoza 2014).

Potential negative or non-target effects of introduced agents have not always been considered. In the early days, many vertebrate species, such as mongoose, cats, and stoat, were introduced to control other non-native vertebrates and became invasive with disastrous non-target effects (Simberloff 2012; Pyšek et al. 2017). A clear message from these introductions is that generalist predators have far too many acceptable prey species to be used to target a specific "pest." For weed control, more recent recognition of the importance of species of conservation or biodiversity value has influenced the attitude to non-target attack of other plant species. As a consequence, regulations for host range testing have become more stringent.

Howarth (1991) reviewed the environmental impacts of biological control programs and documented the negative impacts that had occurred. Generalist vertebrate and insect predators and parasitoids had negative impacts on non-target species, and at least 100 species were considered to have become extinct as collateral damage of biological control programs. Most of these non-target effects were on islands and in freshwater, but the evidence was often hearsay and correlative. More explicit, quantitative, retrospective analyses of non-target effects are required to fully evaluate past efforts and to provide guidance for future biological control programs (Follett et al. 2000).

A review by Louda et al. (2003a) of non-target impacts of classical biological control agents considered ten case histories, three involving weeds and seven involving insect control programs. These histories represent early programs in which host range testing, particularly for predators and parasitoids, was less stringent. This research re-ignited a wave of criticism of biological control introductions (Louda et al. 2003b; Simberloff 2012) and created an era of "skepticism" often based on misconceptions (Denslow and D'Antonio 2005) that lasts to this day.

Concerns with non-target impacts of biological control agents have led to discussion and consideration of increased regulations and assessments of biological control introductions (Denslow and D'Antonio 2005; De Clercq et al. 2011). In the USA, the introduction of agents for the biological control of insects has declined since the mid-1990s (Warner et al. 2009), reflecting the era of skepticism. Several reviews have shown that increasingly stringent regulations would have prevented the introductions of very successful agents that have not subsequently had negative environmental impacts. For example, the *Chrysolina* beetles introduced to control St. John's wort, *Hypericum perforatum*, is New Zealand's most successful weed biological control program and would not have been approved with today's host testing regulations (Groenteman et al. 2011). Hinz et al. (2014) carried out a similar retrospective analysis for five successful weed programs in the USA and came to a similar conclusion: the agents would not have been approved and yet they have not had major non-target impacts. Thus, the desire for a balance between stringent regulations and achieving successful biological control of weeds may be threatening the positive ecosystem services that can be gained through biological control.

Here, we consider more recent information on the ecological impacts of introduced biological control agents that relate to their status as valuable control agents or as invasive species.

12.3 Non-target Effects of Biological Control Agents

12.3.1 Control of Weeds by Insects

Classical biological control of weeds has had few non-target effects, undoubtedly because of the long history of careful host specificity testing (Paynter et al. 2015). Suckling and Sforza (2014) found that of 512 agents evaluated, 92 % had no recorded non-target impacts, and only 0.8 % (4 species) had moderate (plant reproduction reduced and some death from attack) to massive (plants killed before reproduction) impacts on non-target native plant species. Less well quantified are the long-term impacts of this damage on plant population densities (Myers and Sarfraz 2017).

The moth *Cactoblastis cactorum* from South America was initially introduced to Africa and Australia to control *Opuntia* cactus but was later introduced to the Caribbean. The possible movement of the moth from there to North America was not considered initially (Hight et al. 2002). Now established in Florida, *C. cactorum* attacks both rare and native cacti and has the potential to move to areas of rich cactus diversity in southwestern USA, Mexico, and Central America (Pyšek et al. 2017). However, a recent study monitored populations of two of the more common cactus species, *Opuntia stricta* and *O. humifusa*, in Florida and found a relatively high attack by *C. cactorum*, but also relatively high survival and growth of attacked plants (Jezorek et al. 2012). The authors conclude that the assumption that *C. cactorum* will always have severe negative effects on populations of *Opuntia* spp. is not warranted.

The seedhead feeding weevil *Rhinocyllus conicus*, in addition to attacking the target weed musk thistle *Carduus nutans*, also attacks native *Cirsium* thistles in North America (Louda et al. 1997). The impact of this species is site dependent as it is a successful biological control agent at some, but not all, sites in North America (Shea et al. 2005; Marchetto et al. 2014). In addition to the non-target impacts of *R. conicus* on seed production and potentially on population density in *Cirsium* thistles that are seed-limited species (Louda et al. 2003a), *R. conicus* also competes with native insect herbivores on the thistles (Rand and Louda 2012).

Larinus planus, a weevil species that was accidentally introduced to North America from Europe and redistributed for control of the Canada thistle *Cirsium arvense*, also attacks native thistles in North America with moderate impacts (Suckling and Sforza 2014). Although the increase in seed predation by *L. planus* on the threatened species (Pitcher's thistle, *Cirsium pitcheri*) was modest, the low potential for population growth of Pitcher's thistle means that this impact could cause extinction of populations (Havens et al. 2012).

A fourth species found to attack thistles is *Trichosirocalus horridus*, a rosette-feeding weevil introduced as a control agent on musk thistle. In Australia, in addition to *R. conicus*, *T. horridus* was necessary for the reduction of musk thistle density (Shea et al. 2005). In North America, the impacts of this species on musk thistle are mixed, but it also attacks native *Cirsium* thistles, including the tall prairie thistle *Cirsium altissimum* (Wiggins et al. 2009). Its impacts on plant density are not known.

12.3.2 Control of Insects by Insects

Particularly problematic in classical biological control of insects has been the introduction of generalist predators, predominantly species of coccinellids, and generalist parasitoids with multiple generations a year. However, overall non-target attacks are low. Louda et al. (2003a) report that in Hawai'i, 7 % of 59 predators and 10 % of 115 parasitoids have attacked native, non-target hosts, and in North America 16 % of 313 parasitoids use native host species. However, use does not necessarily mean a negative impact on the populations of those non-target species.

A difference between non-target attack of predators and parasitoids, as compared to herbivores, is that the former kill their hosts whereas the latter most frequently reduce the vigour or reproductive capacity of the host. Parasitoids are known to be able to regulate host populations while herbivores can limit host populations to lower densities, but rarely, if ever, regulate plant populations. Non-target attack of predators and parasitoids is probably more difficult to evaluate, particularly in the field, and thus often must be based on experiments using deployed hosts or laboratory trials with non-target hosts and prey.

A tachinid fly, *Compsilura concinnata*, was introduced from Europe to North America in 1906 against the gypsy moth *Lymantria dispar* and the browntail moth *Euproctis chrysorrhoea* (Elkinton and Boettner 2012). This fly is not host specific, has several generations a year, and has had widespread, non-target impacts on a variety of moth hosts, particularly giant silk moths (e.g., *Hyalophora cecropia*). The impact of *C. concinnata* on gypsy moth populations is variable, although experiments carried out in Massachusetts showed that it could be more effective than previously had been thought. In comparison, however, *C. concinnata* impact on the browntail moth in inland sites in Massachusetts is considerably greater and was considered to be responsible for the disappearance of that invasive host species there (Elkinton and Boettner 2012). Thus, this very invasive parasitoid, which has spread across North America, has some positive impacts in reducing a non-native target host species. The full impacts of this invasive parasitoid, both positive and negative, are not known.

The braconid parasitoid *Cotesia glomerata* was introduced to North America as a classical biological control agent against the European cabbage white butterfly *Pieris rapae.* Population declines and range contractions of the native pierid butterfly *Pieris oleracea* in New England in the twentieth century were thought to have been associated both with competition from the introduced *P. rapae* and with attack from the introduced parasitoid *C. glomerata* (Herlihy et al. 2014). In 2001, 100 % of deployed *P. oleracea* were parasitized by *C. glomerata*, but by 2010 only approximately 9 % of test *P. rapae* were parasitized by *C. rubecula* and less than 1 % of *P. oleracea* (the native butterfly) were parasitized by either *Cotesia* species. Competition between the more host specific *C. rubercula* and the less host specific *C. glomerata* appears to have greatly reduced the non-target attack in this situation.

In New Zealand, another parasitoid, *Pteromalus puparum*, was introduced for control of cabbage white butterflies and was suspected of having an influence on the populations of the native red admiral butterfly, *Bassaris gonerilla*. A life table study showed that although *P. puparum* and another self-introduced parasitoid attacked the red admirals, the level of mortality was low compared to other factors (Barron et al. 2003). These examples show that detailed studies are required for proper evaluation of non-target effects.

Establishment rates of coccinellids in North America was lower than for most biological control agents (10 %) and problems have been rare, in part because the species released early on had relatively narrow host ranges (Obrycki and Kring 1998). Eleven species of non-native ladybird beetles have established in Europe, all introduced as biological control agents. In North America, 18 species have established, although it is not clear whether these were a result of the original biological control releases or accidental introductions. Several of these species are now considered to have negative ecological effects. Predators introduced in classical biological control programs have the potential to feed on the target insect pest and non-target herbivores, as well as other predators of the pest. Given the number of introduced ladybird species, this intraguild predation is a potential outcome of the use of ladybirds for biological control. This observation might disrupt biological control and have more far-reaching effects on the native fauna.

In North America the widespread distribution of the European seven-spot ladybird, C7 *Coccinella septempunctata*, has been viewed as potentially having an impact on indigenous ladybird species. More recently, this has been superseded by the Asian harlequin beetle, *Harmonia axyridis*, another invasive species that is also increasingly becoming a problem in Europe (Pyšek et al. 2017). The main issue with invasive ladybirds is the apparent displacement of native ladybirds. Several surveys in North America have shown declines in indigenous coccinellids, starting in the 1990s following the establishment of the seven-spot ladybird, and more recently with the rapid rise in numbers of the harlequin beetle (Evans et al. 2011). However, although there is clear evidence for a large increase in invasive ladybird populations and a concurrent decline in native species, proving the mechanistic link is less easy. A recent study of a 24-year data set in Michigan implicated habitat compression caused by competitive exploitation as the likely cause of native species declines (Bahlai et al. 2015), and other factors, such as changes in land use, could also produce similar patterns (Evans et al. 2011). *Harmonia axyridis* has higher attack and escape rates than the seven-spot ladybird, and intraguild predation is inversely related to aphid densities (Koch 2003); this could contribute to the declines in seven-spot ladybird populations that are making that species less invasive.

12.3.3 Microbial Controls of Weeds, Insects, and Mammals

Although the majority of biological control agents, particularly those used in classical biological control, are invertebrates, pathogens have also been developed as biological control agents. Predominantly, these have been viruses, fungi, and bacteria used to control insect populations, although pathogens, mainly fungi, have been developed for plant control and suppression of plant pathogens (through antagonistic interactions). Some viruses have been used to control invasive vertebrate species. As might be expected, host range testing is an important part of the process before any pathogen release, and overall this process appears to have been very successful.

In a review of 131 recorded classical biological control introductions using 45 insect pathogens and nematodes, and involving 76 target insect species (64 % invasive), no documented cases were found in which a pathogen introduced for insect control caused negative, non-target, or environmental impacts (Hajek et al. 2007). Approximately half the introduced species became established.

For biological control of weeds, Barton (2012) reported that 28 species of fungi involved in 38 classical biological control projects have been introduced worldwide. Six of these have attacked non-target species, but in all cases the non-target attack was predicted in pre-release trials and judged to be minor. More than half of the projects have reduced the densities of the target weeds.

Release of vertebrate pathogens for control of invasive species has, not surprisingly, been rare, but in the three successful cases where viruses were released and established, myxomatosis and rabbit haemorrhagic disease for rabbits in Australia and feline panleukopenia for cats on a sub-Antarctic island, there have been no non-target effects or host range expansion (McColl et al. 2014; but see Morand 2017). Highly specific microbial biological control agents do not appear to be invasive.

12.4 Spill-over Effects

Another type of non-target impact of a biological control agent is a "spill-over effect," the attack by the control agent of non-target species in the vicinity of high densities of the target weed or insect (Morand 2017): this can be a transient effect of unnaturally high densities of a control agent in release areas. A recent empirical example of this in biological weed control involves the target rangeland weed hounds tongue, *Cynoglossum officinale*, and the European root feeding beetle, *Mogulones crucifer* (Catton et al. 2015). This agent was approved and released in Canada in 1997 where it has been suppressing populations of hounds tongue. However, in the USA the release was banned as it had shown low levels of attack of native species in the Boraginaceae. Catton et al. (2015) experimentally tested the level of attack by *M. crucifer* in patches with high hounds tongue density and lower density of a non-target host, *Hackelia micrantha*, over several years. Although initially, non-target plants received eggs and were attacked by *M. crucifer*, the level of attack declined rapidly in subsequent years. They conclude that this agent is safe for biological control introductions even though its host range is broader than is usually acceptable. Because it is an effective agent, densities of both beetles and plants will decline and reduce the opportunity for "spill over." The restriction against the release of *M. crucifer* in the USA potentially represents a lost opportunity, but given sufficient time it is likely that *M. crucifer* will spread from Canada into the USA. Thus, *M. crucifer* might be considered to be an invasive species in the USA, but in Canada it is a successful biological control agent.

12.5 Indirect Negative Effects

In addition to negative impacts of biological control agents exemplified by the attack of non-target hosts, other environmental interactions may occur that have caused some to criticize biological control. For example, two gall flies, *Urophora affinis* and *Urophora quadrifasciata*, released for biological control of diffuse and spotted knapweed, *Centaurea diffusa* and *Centaurea stobe*, reached high densities in many areas of northwestern North America without reducing the densities of the target weeds. The larvae and pupae of these flies became a good winter food source for deer mice, *Peromyscus maniculatus*, and caused their populations to increase (Pearson and Callaway 2006). Pearson and Callaway (2006) suspected that increases in deer mice in rangelands would increase human cases of Hanta virus as an environmental cost of a biological control introduction. The proportion of deer mice that were seropositive for Hanta virus was marginally significantly associated with the higher density of deer mice in areas with *Urophora*. Given that Montana, where this study was done, only has an average of two cases of human infection with Hanta virus in a year, and that the virus is spread by dust usually associated with enclosures such as cabins, the claim that *Urophora* in rangeland will increase Hanta infection in humans is greatly exaggerated. Such speculation, however, garnered considerable media attention and tarnished the reputation of biological control. The subsequent successful biological control of knapweeds by *Larinus minutus* and *Cyphocleonus achates* has greatly reduced the density of *Urophora* spp. (Seastedt 2015), and thus food for populations of deer mice, bringing an end to this hypothetical threat. These successful control agents have received far less public attention than that aroused by the initial fear-mongering regarding Hanta virus.

Another weed biological control program that has received considerable attention in regard to environmental indirect effects is that of the Eurasian saltcedar, *Tamarix* spp., and the introduced beetles, *Diorhabda* spp. Saltcedar was originally introduced for erosion control and subsequently invaded to form dense stands along rivers and streams in southwestern USA. It was considered to be an environmental problem because of its high water use. In addition, saltcedar displaced native willows and cottonwoods as nesting habitat for a number of birds and shade and shelter for other animals, such as toads, lizards, and snakes. Defoliation of saltcedar by the introduced beetles is increasing tree mortality, and this could at least temporally influence these native animals (Seastedt 2015). This is an interesting system in terms of ecosystem impacts of the saltcedar versus potential benefits of biological control. Continued study is required for future evaluation of the status of the ecosystem services of this biological control program.

12.6 Biological Control Contributions to Ecosystem Services

Proper evaluation is necessary to allow an assessment of the positive contributions of biological control to ecosystem services as compared to the potential negative environmental influences. Van Driesche et al. (2010) reviewed 70 classical biological control programs that were carried out to protect natural systems. They concluded that of 21 insect control programs, 81 % provided benefits to biodiversity and 48 % protected products harvested from the natural system, such as water availability, recreation, grazing, fishing, and hunting. For 49 projects targeting invasive weeds, 98 % benefited biodiversity, 47 % protected products, and 25 % preserved ecosystem services. These benefits were obtained even though not all target pests were considered to be completely successfully controlled (i.e., 62 % of insect projects and 27 % of weed projects). Examples of biodiversity benefits arising from biological control targeting pest insects include the control by the lady beetle, *Hyperaspis pantherina*, of the South American scale, *Orthezia insignis*, that was attacking the endangered, endemic gumwood trees on St. Helena, whereas for weed biological control, the weevil *Oxyops vitiosa* and the psyllid *Boreioglycaspis melaleucae* have reduced densities, reproduction, and damage to wildlife caused by the paperbark trees, *Melaleuca quinquenervia*, in wetlands in Florida and the Caribbean (Van Driesche et al. 2010).

Although successful biological weed control is often evaluated by a reduction in density, this does not always translate into improved ecosystem services when appropriate evaluations are done. For example, the reduced density of diffuse knapweed, following the successful establishment of *Larus minutus*, was followed by an increase in non-native grasses, particularly cheat grass, *Bromus tectorum*, in British Columbia (Stephens et al. 2009). Similarly, declines in purple loosestrife, *Lythrum salicaria*, are often followed by increases in reed canarygrass, *Phalaris arundinacea*, (Hovick and Carson 2015). Although many biological control introductions have reduced the invasive target without negative side effects, efforts to quantify the ecosystem-level impacts of these introductions are often not rigorous.

12.7 Conclusions

Invasive species can be detrimental to native systems by reducing biodiversity, productivity, and environmental integrity. One approach to alleviating these impacts is classical biological control, which has the advantage of replacing toxic insecticides and herbicides as well as providing permanent control. Biological control introductions in general have had a good safety record and have contributed to reducing the impacts of targeted invasive species and reestablishing functioning ecosystems. They do, however, add more potentially invasive species to the native system. Increasing our understanding of species interactions and evaluation of agent effectiveness are the keys to predicting what will yield good outcomes (van Wilgen et al. 2013). Crucial to making biological control a science is post-release, quantitative measurement of both the positive contributions and possible negative impacts of each introduced species. This criterion could involve direct or indirect effects, for example, if the control agent serves as a host for native predators or if parasitoids also attack native species. Both positive and negative impacts must be kept in perspective to avoid lost opportunities for future biological control programs or unnecessary additional introductions.

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Chapter 13
Disruption of Pollination Services by Invasive Pollinator Species

Carolina L. Morales, Agustín Sáez, Lucas A. Garibaldi, and Marcelo A. Aizen

Abstract Plant–pollinator interactions and associated pollination services are essential for crop production and the integrity of terrestrial ecosystem services. Introduced pollinators, in particular social bees such as honeybees and bumblebees, have become invaders in many regions of the world, strongly affecting the pollination of native, cultivated, and non-native plants. These effects can be direct, when invaders interact with local flowering plants, or indirect, when invaders modify the interaction of native pollinators with flowering plants. Direct effects on pollination depend on whether the plant benefits from the flower visits are greater than their costs, a relationship that can be density dependent. Shifts from mutualism to antagonism occur when invasive pollinators reach extremely high densities, because the interaction costs exceed the benefits. Indirect effects depend on whether pollinator invaders alter the benefit–cost ratio of native pollinator visits, displace them, or trigger reductions in native pollinator diversity. Through a literature review, we found that the impacts of invasive pollinators on pollination were predominantly negative for native plants, mixed for crops, and positive for invasive plants. Furthermore, they can synergistically interact with other stressors on pollination such as climate change and habitat disturbance. Although invasive pollinators can back up pollination of some native plants in highly disturbed habitats, and some crops in intensively modified agro-ecosystems, they cannot replace the role of a diverse pollinator assemblage for wild plant reproduction and crop yield. Hence, managing agro-ecosystems for enhancing wild pollinator diversity, and avoiding further introductions of non-native pollinators, are realistic cost-effective measures for the provision and stability of pollination services.

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13.1 Introduction

Pollination services contribute directly and indirectly to human welfare. Biotic pollination, the transfer of pollen between flowers by free-living animals, contributes to the sexual reproduction of approximately 90 % of the flowering plants (Angiosperma) (Ollerton et al. 2011) and increases fruit or seed quality or quantity of about 70 % of the major crops worldwide (Klein et al. 2007). Furthermore, 5 % to 8% of the global crop production for human consumption can be lost directly in the absence of animal pollination (Aizen et al. 2009), and many crops, from which vegetative parts are harvested, rely on pollinators for breeding and seed production. Indeed, animal pollination is a key ecosystem service, with plant–pollinator interactions having a significant role in maintaining the integrity of most terrestrial ecosystems, indirectly allowing the delivery of other ecosystem services such as primary production and carbon sequestration.

Invasive species are one of the main drivers of anthropogenic global change. As such, they can substantially disrupt the capacity of ecosystems to deliver services, including pollination (Traveset and Richardson 2006; Schweiger et al. 2010). Many bee species of diverse genera have become established in the wild out of their ranges as a consequence of accidental or intentional introductions (Goulson 2003; Bartomeus et al. 2013). For instance, some cavity-nesting species have been accidentally transported together with their host materials (e.g., *Anthidium manicatum*; Gibbs and Sheffield 2009), whereas other cavity-nesting species (e.g., *Megachile* and *Osmia*), as well as social or colonial genera *Apis* and *Bombus*, have been intentionally introduced for pollination purposes (Goulson 2003; Gibbs and Sheffield 2009; Schweiger et al. 2010). However, only a small fraction of these introduced species became "invasive species", that is, with individuals dispersing, surviving, and reproducing at multiple sites across a greater or lesser spectrum of habitats and extent of occurrence (Blackburn et al. 2011). Moreover, according to a literature survey that identified 403 primary research publications that investigated the ecological effects of invasive insects (Kenis et al. 2008), only 4 of 72 species were pollinators (*Megachile rotundata*, *M. apicalis*, *Apis mellifera*, *Bombus terrestris*), with only *A. mellifera* and *B. terrestris* demonstrating ecological impacts in the field (cf. the impact of an invasive solitary orchid bee on an invasive plant reproduction) (Table 13.1).

The massive and unquestioning active introduction of honeybee, *A. mellifera* hives is still occurring, whereas that of bumblebee colonies (*Bombus* spp., in particular *B. terrestris*) is just beginning (Fig. 13.1). Both introduced bumblebees as well as African honeybees (Box 13.1) continue to expand their ranges in the Americas at surprisingly high rates. Therefore, a comprehensive revision of the consequences of these pollinator invasions on pollination services is both timely and necessary.

Fig. 13.1 Introduced pollinators that have become invasive in different parts of the world: *Bombus terrestris* (**a**), *Bombus ruderatus* (**b**), and *Apis mellifera* (**c**) (Photograph by Agustín Saez (**a**), Carolina L. Morales (**b**), and Natacha Chacoff (**c**))

Box 13.1: Invasion History of Honeybees in the Americas

The natural range of the western honeybee, *Apis mellifera*, extends from northern Europe to southern Africa, and from the British Isles to the Ural Mountains, western Iran, and the Arabian peninsula. More than 25 subspecies of honeybees are recognized. The African honeybee, the subspecies *A. mellifera scutellata*, originally occurred in southern Africa and was first introduced to Brazil in the 1950s with the aim to establish honeybee populations better adapted to tropical conditions. Since introduction, this subspecies has spread through tropical and subtropical Americas, from northern Argentina to southwestern USA, being considered one of the most successful cases of biological invasions (Schneider et al. 2004).

The African honeybee initially interbred with other European honeybee subspecies, such as the Italian *A. m. ligustica* and the Iberian *A. m. iberiensis*, also introduced in America, producing the hybrid commonly known as "Africanized honeybee." However, although substantial hybridization occurs when African honeybees invade areas with populations of European

(continued)

Box 13.1 (continued)

subspecies, European characteristics tend to be lost over time, and through much of its invaded range in the New World, African characteristics have been preserved (Schneider et al. 2004). The terminology used to name and describe the descendants of *A. mellifera scutellata* in the New World is highly controversial. In this chapter we refer to them as “African honeybees” and use the term “feral” to refer to populations established in the wild, in opposition to “managed” for those being kept in bee hives.

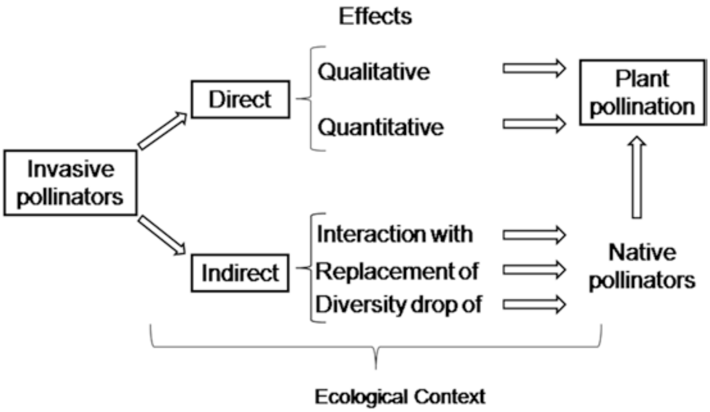

Fig. 13.2 Diagram representing the direct and indirect effects of invasive pollinators on plant pollination

This chapter reviews the impacts of introduced invasive pollinators in the broad sense on flower-visiting animals, and on native pollinators and pollination services. The conceptual framework we present includes direct and indirect effects, wherein direct effects are characterised by the benefit–cost balance of the interaction between the invasive pollinator and a given plant, which in turn takes into account its per capita (qualitative) effect and its mass (quantitative) effect (Fig. 13.2). Indirect effects occur additionally when this novel pollinator impacts the pollination of a given plant, either by their interaction with the native flower visitors, by replacing efficient pollinators, or by driving reductions in pollinator diversity. These effects will ultimately be strongly influenced by the ecological and community context, including their interaction with other environmental stressors such as climate change, habitat disturbance, and invasive plants (Fig. 13.2). The main mechanisms behind these impacts are illustrated in this review, using examples of diverse taxa of native, cultivated, and invasive plants from different ecosystems worldwide (Table 13.1.

Table 13.1 Effects of invasive pollinators on the reproduction (i.e., fruit or seed set or quality) of native, cultivated, or invasive plants with indication of the demonstrated or proposed mechanism of interference

Region	Invasive pollinator	Plant species (family)	Major pollinators	Effect	Putative mechanism	Reference
Native plants						
New Wales	AM	*Dillwynia juniperina* (Fabaceae)	*Lasioglossum* sp., *Leioproctus* sp.	(0)	Per visit efficiency of AM similar to native species	(1)
North Queensland	AM	*Melastoma affine* (Melastomaceae)	*Lestis bombylans, Nomia* sp., *Amegilla anomala, Xylocopa* near *gressitti*	(−)	Decreased pollen deposition and increased pollen removal from stigma	(2)
East Brazil	AM	*Clusia arrudae* (Clusiaceae)	Solitary bees	(−)	Increased pollen removal from male flowers	(3)
North Brazil	AM	*Dinizia excelsa* (Fabaceae)	Stingless bees	(+)	Increased gene flow distance	(4)
Mauritius	AM	*Sideroxylon cinereum* (Sapotaceae)	White-eye birds	(−)	Reduced efficiency in pollen transfer	(5)
		S. puberulum (Sapotaceae)				
Japan	BT	*Corydalis ambigua* (Papaveraceae)	Bumblebees	(−) (0)	Reduced legitimate visitation by invader and probably by native species when flowers are robbed by BT	(6)
		Primula japonica (Primulaceae)		(+) (−)		
		Polygonatum odoratum (Liliaceae)		(−) (−)		
		Cirsium kamtschaticum (Compositae)		(0) (0)		
		Ligustrum obtusifolium (Oleaceae)		(−)		
		Adenophora triphylla (Campanulaceae)		(0) (−)		
		Hosta sieboldi var. *rectifollia* (Liliaceae)		(0) (−)		

(continued)

Table 13.1 (continued)

Region	Invasive pollinator	Plant species (family)	Major pollinators	Effect	Putative mechanism	Reference
Japan	BT	*Corydalis ambigua* (Papaveraceae)	*Bombus ardens*	(−)	Reduced legitimate visits of flowers robbed by BT	(7)
			Bombus hypocrita			
South Argentina	AM	*Chlorea virescens*, *Brachystele unilateralis* (Orchidaceae)	*Bombus dahlbomii*	(+)	Increased visitation frequency	(8)
	BT					
	BR					
South Argentina	BR	*Alstroemeria aurea* (Alstroemeriaceae)	*Bombus dahlbomii*	(+) (−)	Increased visitation but reduced per-visit efficiency in transferred pollen quantity and quality	(9)
Cultivated plants						
South México	AM	*Coffea arabica* (Rubiaceae)	Native bees and managed honeybees	(−)	Reduced diversity	(10)
North Argentina	AM	*Citrus paradisi* (Rutaceae)		(+)	Almost unique pollinator observed	(11)
Australia	AM	*Macadamia integrifolia* (Proteaceae)	*Trigona carbonaria*	(?)	Almost unique pollinator observed, but no significant relationship between visitation and fruit set	(12)
South Argentina	BT	*Rubus idaeus* (Rosaceae)	Managed honeybees and native bees	(−)	Rupture of styles by excess of visits	(13)

Invasive plants						
Western USA	AM	*Centaurea solstitialis* (Asteraceae)	Native halictidae bees and introduced *Megachile apicalis*	(+)	Most frequent visitor	(14)
Tasmania	AM	*Lupinus arboreus* (Fabaceae)	Bumblebees	(+)	Unique pollinators large enough to manipulate flowers	(15)
	BT					
Southeast USA	*Euglossa viridissima*	*Solanum torvum* (Solanaceae)	Native halictid bees	(+)	Most efficient pollinator and most frequent in forest sites	(16)

Two different symbols means that two different outcomes were reported for different variables. In (4), (10), and (11) AM refers to the African honeybee (see Box 13.1). AM *Apis mellifera*, BT *Bombus terrestris*, BR *Bombus ruderatus*, (−) negative, (+) positive, (0) neutral, (?) uncertain

References: (1) Gross CL (2001) Biol Conserv 102:89–95; (2) Gross CL, Mackay D (1998) Biol Conserv 86:169–178; (3) Carmo RM, Franceschinelli EV, Silveira FA (2004) Biotropica 36:371–376; (4) Dick CW (2001) Proc Biol Sci 268:2391–2396; (5) Hansen DM, Olesen JM, Jones CG (2002) J Biogeogr 29:721–734; (6) Kenta T, Inari N, Nagamitsu T, et al. (2007) Biol Conserv 134:298–309; (7) Dohzono I, Kunitake Y, Yokoyama J, Goka K (2008) Ecology 89:3082–3092; (8) Sanguinetti A, Singer RB (2014) Biol Conserv 175:10–20; (9) Madjidian JA, Morales CL, Smith HG (2008) Oecologia (Berl) 156:835–845; (10) Badano EI, Vergara CH (2011) Agric For Entomol 13:365–372; (11) Chacoff NP, Aizen MA, Aschero V (2008) Proc Biol Sci 275:907–913; (12) Blanche KR, Ludwig JA, Cunningham SA (2006) J Appl Ecol 43:1182; (13) Sáez A, Morales CL, Ramos LY, Aizen MA (2014) J Appl Ecol 51:1603–1612; (14) Barthell JF, Randall JM, Thorp RW, Wenner AM (2001) Ecol Appl 11:1870–1883; (15) Stout JC, Kells AR, Goulson D (2002) Biol Conserv 106:425–434; (16) Liu H, Pemberton RW (2009) Oecologia (Berl) 159:515–525

13.2 Direct Effects of Invasive Pollinators on Plant Pollination

13.2.1 Per Capita Effect

Plant–pollinator interaction can be viewed as a benefit–cost relationship, which can be mutualistic or antagonistic, depending on whether the net benefit (benefit minus cost) is positive or negative (Aizen et al. 2014, and references therein). From the perspective of a plant, the benefit obtained from a single flower visit is the transfer of high-quality conspecific pollen from anthers to stigma, and the cost involves the removal of floral rewards (nectar and pollen), flower damage, and the transfer of pathogens, among other matters. Invasive pollinators can disrupt the pollination of native plants, if the per-visit costs exceed the benefits. Trait matching between interacting partners is expected to enhance benefits (pollen transfer) while minimizing costs (pollen wastage and flower damage) (Schleuning et al. 2015).

Experimental manipulation of the identity of flower visitors in isolated plants has been a powerful tool to estimate the net benefit provided by alternative pollinators. For example, in native *Dillwyinia juniperiana*, the probability of a flower setting fruit after a single visit did not significantly differ between honeybees and native bees; however, fruit set was 10 % greater when native bees were the only visitors compared to honeybees (Table 13.1). In Japan, where *Bombus terrestris* has become a widespread invader, seven native bumblebee-pollinated plant species were experimentally exposed to different treatments, simulating different invasion scenarios where *B. terrestris* was absent ("native" treatment), coexisted with native bumblebees ("mixed" treatment), or completely replaced them ("non-native" treatment) (Table 13.1). Five of seven species experienced reduced fruit set, fruit quality, or both, but only one species experienced increased fruit quality in the non-native versus native treatment. Visits by *B. terrestris* were of lower effectiveness (i.e., fruits per visit) than those of the native bumblebee because of physical mismatching between the length of the *B. terrestris* tongue and the length of the native plant corollas. Therefore, the per capita effect of a new interacting partner (invasive pollinator) on a plant pollination can vary according to the degree of matching between pollinator and plant traits.

13.2.2 Mass Effect

Invasive species typically reach much higher abundances than those observed in their native ranges or than their native counterparts in invaded regions (e.g., European and African honeybees; *B. terrestris* in South America and Japan and *B. ruderatus* in South America). These high abundances lead to unusually high visitation frequencies to flowers. As an example, Fig. 13.3 shows the distribution of visitation frequencies in eight plant–pollinator webs across different forest habitat types in southern Argentina, where only interactions with native pollinators are

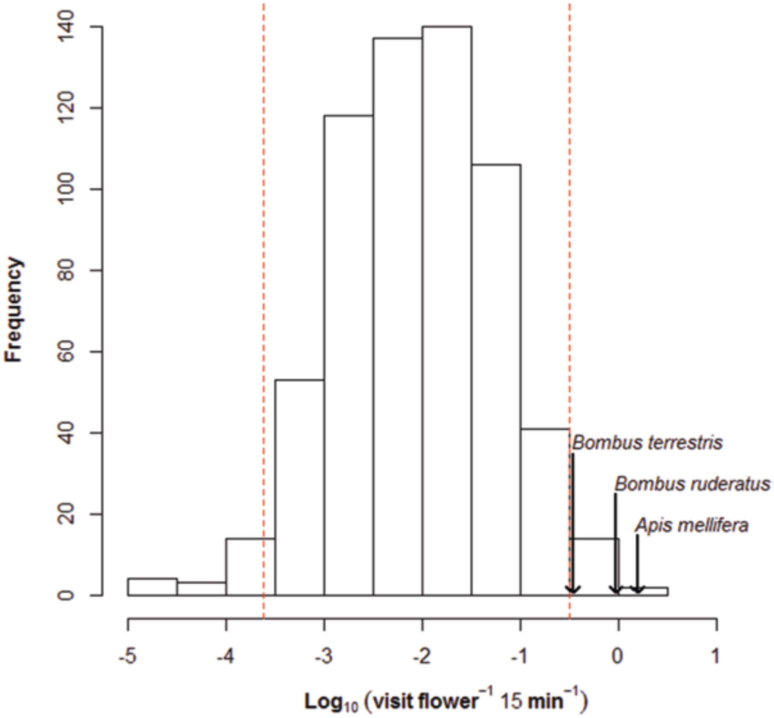

Fig. 13.3 Mean annual visitation rate of native pollinators on plants across eight forest habitat types in Southern Argentina. The *dashed line* represents the percentiles 2.5 and 97.5 of the frequency distribution. The *arrows* at the *right* side of the graph indicate the highest mean annual visitation rate achieved by the three invasive pollinator species in this area, namely, *Bombus terrestris* in *Alstromeria aurea*, *B. ruderatus* in *Carduus nutans*, and *Apis mellifera* in *Cirsium vulgare* (Data from Aizen et al. 2008, supplementary material, and Morales et al. 2013)

included. By contrast, the thick arrows indicate the maximum visitation frequency recorded for a plant–pollinator interaction in which invasive pollinators are involved. This histogram clearly illustrates how invasive pollinators tend to participate in interaction frequencies that are higher than "normal".

According to the benefit–cost conceptual model proposed by Aizen et al. (2014), benefits of the plant–flower visitor interactions increase asymptotically with interaction frequency while costs increase linearly (Fig. 13.4). Hence, from the perspective of the plant, a shift to antagonism from an otherwise mutualistic plant–animal interaction is especially prevalent when partners have disparate relative densities (Aizen et al. 2014). Therefore, the impact of this increase in interaction frequency will depend on whether, within the range of frequencies observed, interaction costs exceed their benefits.

Following the Aizen et al. (2014) conceptual model, Fig. 13.4 shows the expected density-dependent benefit–cost relationship between a plant species and two pollinator species that differ both in their interaction costs (straight lines) and their benefits (asymptotic curves). At any frequency, interactions with invasive pollinators

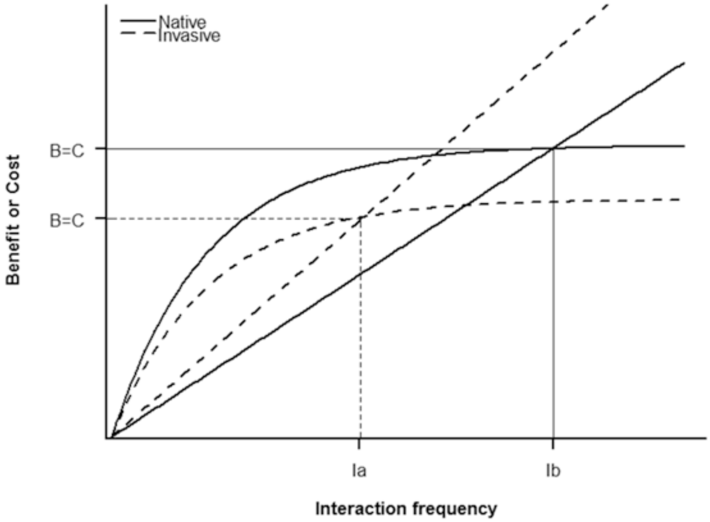

Fig. 13.4 Plant benefits (*B*) and costs (*C*) of increasing interaction frequency (*I*) from native (*solid lines*) or invasive (*dashed lines*) pollinators. Benefits (e.g., seed set) increase nonlinearly and are expected to be greater from native than invasive pollinator visits, whereas costs (e.g., flower damage) increase linearly and are expected to be lower from native pollinator visits. Invasive pollinators are mutualists when $I < Ia$ (benefit > cost) and antagonists when $I > Ia$ (benefit < cost). Native pollinators are mutualists when $I < Ib$ and antagonists when $I > Ib$. If invasive pollinators become too abundant, they are expected to behave mostly as antagonists from the perspective of the plant

that provide lower benefits and entail higher costs than interactions with the average native pollinator are expected to result in a lower net benefit. Moreover, mutualism is expected to switch into antagonism at a lower interaction frequency when the plant interacts with an invasive pollinator (*Ia*) than with an average native pollinator (*Ib*). Conversely, when the abundance of floral resources is high relative to visitors, the density of invasive flower visitors is expected to be within the range of increasing net benefits (Aizen et al. 2014). This situation frequently occurs during short periods in agricultural landscapes when mass flowering crops provide a high abundance of floral resources. In such cases, increases in visitation frequency are expected to benefit yields in pollen-limited crops.

In tropical America, the invasion of feral African honeybees seems to have augmented pollination and boosted the yields of coffee, *Coffea arabica*, as suggested by the substantial increase in coffee yield in many neotropical countries. This increase has been partly coincident with the establishment of African honeybees in the region (Roubik 2002, and references therein). However, in the same crop, fruit set was negatively related to African honeybee visitation frequency (Table 13.1; Fig. 13.5a). This result is consistent with a shift in the balance from mutualism to antagonism at excessive visitation frequencies, given that the total number of honeybee foragers per flower appears to be sufficiently high to cause the rapid depletion of floral resources (but see also Sect. 13.3.3). In a temperate crop, an antagonist effect

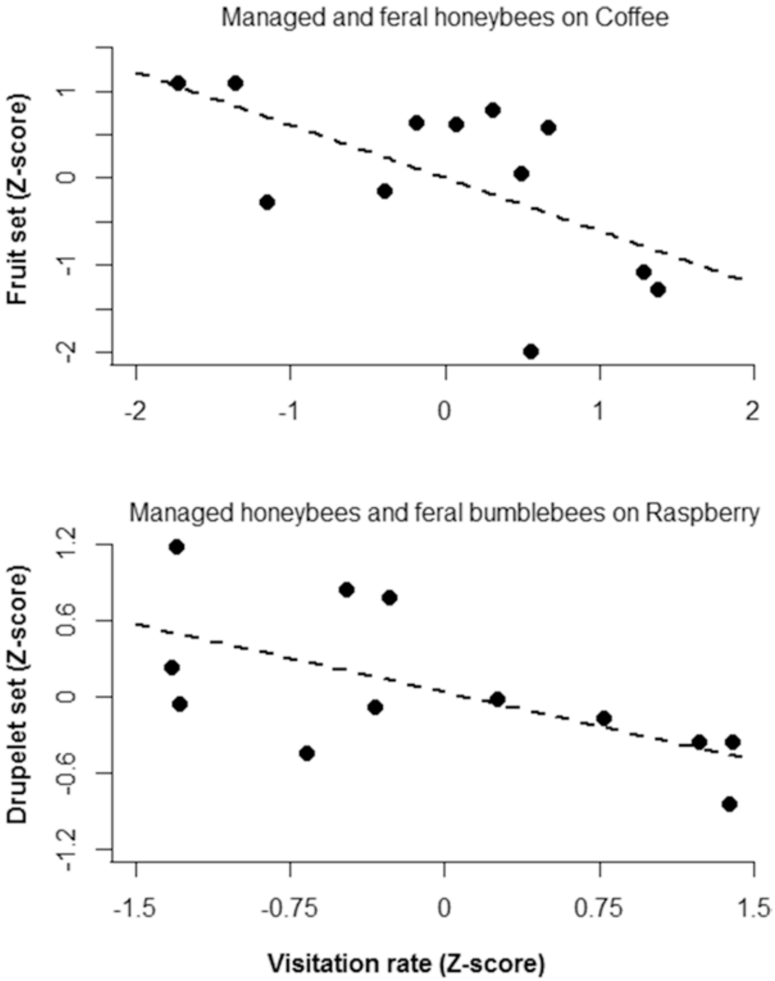

Fig. 13.5 Negative effect of increasing visitation rate of introduced pollinators (both managed and feral) on pollination services in two crop systems: fruit set of highland coffee, *Coffea arabica*, in tropical Southern Mexico (**a**) and drupelet set in raspberry, *Rubus idaeus*, in temperate Southern Argentina (**b**) (Data of coffee in *z*-score values were obtained from Garibaldi et al. (2013) supplementary material, original data from study (10) quoted in Table 13.1; data of raspberry from study (13) quoted in Table 13.1)

of increasing visitation frequency has resulted from a combination of managed honeybees and invasive *B. terrestris* (Table 13.1; Fig. 13.5b), whereas in raspberry fields in Southern Argentina, the exceptionally high abundance reached by *B. terrestris* has translated into visitation frequencies that both saturate benefits (pollen deposition) and increase interaction costs (style damage), thereby shifting the interaction from mutualism towards the antagonism threshold (Aizen et al. 2014).

13.3 Indirect Effects

13.3.1 Impacts Mediated by the Interaction with Native Pollinators

Invasive pollinators can disrupt the pollination of plants by altering the outcome of interactions between plants and native pollinators. This disruption occurs through the modification of the behaviour of the native pollinators by the invasive pollinators. The most obvious mechanism for this is the reduction of visitation by native pollinators in the presence of invaders. For instance, in Mauritius, white-eye birds stop foraging on native Sapotaceae trees when honeybees deplete nectar (Table 13.1). In a Japanese bumblebee experiment, five plant species were exposed to a "mixed" treatment in addition to "non-native" and "native" treatments: the "mixed" treatment caused reduced fruit set and quality for *Primula odorata*, and increased fruit set but reduced fruit quality for *Polygonium japonica*, relative to the "native" treatment (Table 13.1). Thus, in *P. odorata*, reduced visitation by native bumblebees in the "mixed" compared to the "native" treatment suggests that the presence of *B. terrestris* disturbs native bumblebees, which may partly explain reproductive failure, given that legitimate visits is the primary factor explaining reproductive success.

A more subtle mechanism for this interaction is the modification of the costs or benefits provided to plants by native pollinators in the presence of invasive counterparts. For example, in North Queensland (Australia) honeybees not only deposited less pollen per visit than native bees in flowers of the shrub *Melastoma affine* (Table 13.1), but also removed pollen from stigmas previously deposited by native species, which reduces plant reproductive success. In Brazil, pollen-collecting honeybees visiting the native shrub *Clusia arrudae* removed almost all pollen from the male flowers (Table 13.1), leading native solitary bees visiting male flowers previously visited by honeybees to carry on their bodies less than 0.1 % of the pollen grains carried by bees leaving flowers not visited by the honeybee. As a consequence, fruit set was negatively correlated with honeybee visitation to male flowers.

These examples show that the impacts of invasive pollinators can also be mediated by their interactions with native pollinators, triggering changes in the benefits and costs per visit of native pollinators or in the frequency of their visits. Therefore, single-visit experiments in isolated flowers are poor predictors of the overall impacts of invasive pollinators and should be complemented with other experimental and observational approaches.

13.3.2 Impacts Caused by the Replacement of More Efficient Pollinators

Invasive pollinators can outcompete native pollinators through competition for resources, nesting sites, or transmission of pathogens, among other mechanisms (Goulson 2003, and references therein). In relatively specialised plant pollination systems, this can lead to an almost complete replacement of major pollinators by invasive pollinators, whose impact would depend on the relative benefit–cost of the interaction of the invasive pollinator compared to the native pollinator with a given plant (Sects. 13.2.1 and 13.2.2). For instance, the reduced fruit set or fruit quality suffered by five of seven plants experimentally exposed to *B. terrestris* compared to native bumblebees (Table 13.1; Sect. 13.2.1) suggests that the ongoing replacement of native bumblebees by invasive *B. terrestris* can negatively affect the reproduction of native plants.

However, the replacement of major pollinators by invasive pollinators does not always have deleterious effects on the reproduction of native plants, particularly when visits by the major pollinators are too infrequent to fulfil pollination requirements. For instance, non-autogamous deceptive orchids strongly rely on a few specialist pollinator species for their reproduction. *Chlorea virescens* and *Brachystele unilateralis*, two orchids endemic to Southern Argentina and Chile, are unable to set seeds in the absence of pollinators. A 2-year study carried out after a *B. terrestris* invasion, coincidental with the almost functional local extinction of their putative pollinator, *B. dahlbomii*, revealed that, because their flowers were so large, none of the small remaining native pollinators were capable of transferring pollinaria to them (Table 13.1). In addition, invasive *B. terrestris*, *B. ruderatus*, and *Apis mellifera* were responsible for almost all the pollination events observed. Therefore, the unusually high fruiting success in the study area, compared to that reported for other temperate orchid species, might be attributed to the high incidence and visitation frequency of these invasive species (see Sect.13.2.2; Table 13.1).

In the same region, the per-visit benefit provided by invasive *B. ruderatus* to *Alstroemeria aurea* flowers are lower compared to native *B. dahlbomii* because the former deposits less and lower quality pollen than the native species. However, this reduced per-visit efficiency of the invasive species seems to be at least partially compensated by visitation frequencies higher than those historically recorded for the native species (Morales et al. 2013, Table 13.1).

13.3.3 *Impacts of Invasive Pollinators Mediated by Reductions on Native Flower Visitor Diversity*

The effects of pollinator species diversity on pollination services are expected to be mediated by changes in pollinator functional diversity, that is, the among-species variation in behavioural, morphological, and physiological traits relevant to pollination function (Fründ et al. 2013; Gagic et al. 2015). Functional diversity of pollinator assemblages increases the level and stability of pollination services through several non exclusive mechanisms (Tscharntke et al. 2005). First, functional richness and evenness, two components of functional diversity, should enhance niche complementarity, such as differences among flower visitors in temperature preferences or activity periods (Fründ et al. 2013; see also Sects. 13.4.1 and 13.4.2).

Second, functional diversity can enhance pollination services because of "sampling effects", that is, higher diversity of traits associated with higher species diversity increases the probability of finding a particular pollinator species, characterised by a series of traits, which increases the pollination efficiency of one or several particular plant species (Tscharntke et al. 2005; Schleuning et al. 2015). Third, functional diversity can enhance particular interspecific interactions. For example, in almond orchards in the USA, the presence of non-*Apis* bees changed the foraging behaviour of honeybees, which tended to fly more often between tree rows, increasing the pollination effectiveness of a single honeybee visit, resulting in greater fruit set than in orchards where non-*Apis* bees were absent (Brittain et al. 2013). Therefore, pollinator diversity can synergistically increase pollination service through species interactions that alter the behaviour and resulting functional quality of a dominant pollinator species (Brittain et al. 2013). Last, pollinator diversity increases the stability of pollination services even when different pollinators are functionally equivalent because it buffers the demographic vagaries of individual species.

A recent synthesis of pollinator and fruit set surveys from 600 fields involving 41 crop systems revealed that pollinator richness had a positive and significant effect on wild pollinator visitation, which in turn consistently enhanced fruit set in all crop systems without exception. In contrast, honeybee visitation increased fruit set significantly in only 14 % of them (Garibaldi et al. 2013). This finding confirms the global positive effect of pollinator diversity on pollination services.

By displacing native pollinators, invasive pollinators can reduce pollinator diversity. Evidence of such reductions in the diversity of native pollinators resulting from pollinator invasions is mixed, and the cause–effect relationship between the phenomena is often hard to separate from other confounding factors (Sect. 13.4). However, negative effects on native pollinator diversity prevail when invaders become too abundant. For instance, in Tasmania, Goulson et al. (2002) found no effect of *B. terrestris* on native pollinator diversity, but a negative effect of *A. mellifera*, which was by far the most abundant bee species.

Evidences of a shortage of pollination service driven by decreased pollinator diversity as a result of pollinator invasions are even scarcer. In coffee plantations in Mexico, the number of honeybee workers per plantation was negatively correlated with native pollinator diversity and fruit set (Table 13.1; Fig. 13.5a). Although the generality of this type of impact of invasive species should be tested, the foregoing examples illustrate the potential consequences of losses of biodiversity on pollination services.

13.4 Interaction of Invasive Pollinators and Other Drivers of Global Change

Pollination services are under the threat of many stressors, which rarely act in isolation (Schweiger et al. 2010). Rather, they can interact in complex and even nonadditive manners, either modulating or amplifying their individual impacts (González-Varo et al. 2013). Climate change, habitat disturbance, and plant invasions are among these environmental stressors that can interact with invasive pollinators.

13.4.1 Climate Change

The impact of invasive pollinators is influenced by climate change. *Apis mellifera* and *Bombus terrestris* are social and generalist species with broad resource and habitat niches, long foraging seasons, and a widespread distribution within their regions of origin. Therefore, they are expected to be less sensitive to global warming *per se* and concomitant phenological or spatial mismatches than most native pollinators, which are predominantly solitary and on average more specialised (Schweiger et al. 2010). A recent review by Forrest (2015) concludes that, although primarily observational studies suggest that phenologies of co-occurring plants and pollinators tend to respond similarly to the same environmental cue, some interacting species can suffer phenological mismatches. However, the impact on plant reproduction is unknown, largely because of a lack of research.

Invasive pollinators can complement the pollination service provided by native pollinators under increasing temperature and precipitation variability (see Sect. 13.3.3), or compensate for the plant–pollinator mismatches resulting from the spatial or phenological shifts experienced by native pollinators, thus benefitting generalist plants. On the other hand, they are expected to exacerbate the detrimental effect of climate change on highly specialist plant–pollinator systems by increasing the relative competitive ability of invasive over more efficient native pollinators (Sect. 13.3.2).

13.4.2 Habitat Disturbance

Habitat alteration and invasive pollinators can affect native pollinators to the same magnitude by decreasing visitation rates (Montero-Castaño and Vilà 2012). Moreover, invasive pollinators are usually associated with disturbed habitats (Aizen et al. 2008, and references therein), where, given the correlative nature of most ecological studies, the collapse of native pollinators can hardly be attributed to either invasive species or habitat disturbance *per se.* A possible interpretation of these patterns is that invasive pollinators take advantage of habitat disturbance, becoming more successful invaders and therefore competitively superior to native counterparts that are actively displaced by invaders in disturbed habitats. Therefore, habitat disturbance is expected to exacerbate the negative impacts of invasive pollinators on native pollinators. Alternatively, native pollinators might decline as a direct consequence of habitat disturbance, being passively replaced by invasive pollinators that take advantage of niche release. Regardless of the cause–effect relationship, the consequences for pollination services will depend on whether invasive pollinators can compensate for the loss of native pollinators in disturbed habitats. In the Chaco Dry Forest of Argentina, the consistently higher visitation frequency of feral honeybees on plants growing in small forest fragments cannot fully compensate for the loss of native pollinators, but it does seem to ameliorate the magnitude of the negative effects of fragmentation on reproduction of wild plants (Aguilar et al. 2006, and references therein). In the extreme, invasive pollinators can overcompensate for the loss of native pollinators. For instance, in Amazonian rainforests honeybees are the unique pollinators able to fly distances long enough to visit isolated populations of the tropical tree species, *Dinizia excelsa*, that remain in pastures and forest fragments. The trees in these isolated fragments produce higher seed yields than trees growing in the forest because honeybees transported pollen from more distant parents than native pollinators (Table 13.1).

The intensification of agricultural systems is also a strong driver of native pollinator losses (Garibaldi et al. 2014). Various syntheses revealed that the diversity of native pollinators and their abundance in crops negatively correlates with increasing distances from crop borders and decreasing areas of natural and seminatural habitats in the local landscape. Although the detrimental effect on pollination services has also been confirmed (Garibaldi et al. 2014), these impacts seem negligible when feral honeybees are the major pollinators (Table 13.1).

In Australia, stingless bees are important pollinators of macadamia, *Macadamia integrifolia*, but the honeybee has been reported as the almost only pollinator of this crop. This finding was thought to be a result of a potentially higher resistance to pesticides in honeybees compared to the native bees (Table 13.1). Thus, invasive pollinators can back up pollination in extremely disturbed habitats, where the native pollinators are disadvantaged. In any case, an obvious conclusion is that, to support healthy and rich pollinator assemblages on which a diversified and stable pollination service relies, habitat disturbance should be avoided or minimized, and agricultural practices that mitigate the impact of increasing land use intensification should be employed (Garibaldi et al. 2014).

13.4.3 Invasive Plants

The invasion of introduced flowering plants is often pollen limited and, although they can rapidly integrate into local plant–pollinator webs through interactions with native pollinators (Memmott and Waser 2002), when invasive pollinators are present introduced plants tend to interact more frequently with them beyond the effects of habitat disturbance (Aizen et al. 2008).

Differential interactions between invasive plants and pollinators may arise from the fact that invasive pollinators tend to be more generalist than most native pollinators (Memmott and Waser 2002; Aizen et al. 2008), or from a better morphological matching, particularly in large or highly specialised flowers. For instance, in Tasmania native bees are too small to manipulate flowers of the invasive *Lupinus* *arboreaus*, which rely on *A. mellifera* and *B. terrestris* to set seeds (Table 13.1). Similarly, the honeybee also promotes seed set of *Centaurea solticialis* in the USA, because it is larger in size compared to most native bees (Table 13.1). This difference can lead to an "invasional meltdown" (*sensu* Simberloff and Von Holle 1999), increasing the invasive potential of the interacting partners, or exacerbating their individual impacts (Aizen et al. 2008, and references therein).

13.5 Conclusions

Pollination services enhance the sexual reproduction of most flowering plants involved in many terrestrial ecosystem services, and are essential to guarantee diverse and abundant high-quality crop yields, which all together contribute to human well-being. Paradoxically, invasive pollinators can threaten the pollination service for which most of them were primarily introduced. In highly disturbed or intensively managed habitats, where wild and cultivated plants might suffer high pollination limitation, invasive pollinators might ameliorate such a pollination deficit. However, they cannot replace the function of a diverse assemblage of native pollinators. Therefore, avoiding further introductions, as well as managing and restoring agro-ecosystems to improve the habitat conditions needed by wild pollinators to survive (Garibaldi et al. 2014), emerge as the highest priorities to guarantee healthy and long-term pollination services.

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Chapter 14
Impact of Invasions on Water Quality in Marine and Freshwater Environments

Pedro Reis Costa, José Carlos Martins, and Paula Chainho

Abstract Water quality of marine and freshwater environments, including brackish waters, can be highly impacted by the introduction, establishment, and spread of non-native species. Phytoplankton are among the most common arrivals, with the bloom-forming species, such as toxic freshwater cyanobacteria and marine dinoflagellates, being of particular concern. Their massive population increase may lead to water discolouration, reduced transparency, changes in nutrients cycling, events of anoxia, and release of potent toxins contaminating the food web and drinking water. Top-down control that regulates primary productivity is carried out by filter-feeding organisms. Bivalve mollusks are often the dominant filter feeders in many aquatic systems. The high filtration rates of some non-native bivalves may significantly increase the ecosystem filtration capacity, resulting in drastic changes of phytoplankton biomass and composition. Invasive bivalves also have a marked role removing other suspended particles, which result in increasing water clarity with subsequent growth of submerged vegetation. This apparent benefit may not be innocuous because changes in phytoplankton composition may lead to dominance of toxic algae species. Biomagnification of contaminants filtered from the water column, biofouling, and increase of sedimentation are among other detrimental effects associated with the increase of non-native bivalve populations. In this chapter, the main impacts on water quality raised by non-native phytoplankton and bivalve species are reviewed.

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14.1 Introduction

It is estimated that at least 7000 to possibly more than 10,000 species of organisms are in transit in ship ballast waters alone every day. These species include unicellular organisms, invertebrates, and fish (Carlton 1999). Not taking into account bacteria and other microorganisms, phytoplankton and zooplankton species are the most frequent and abundant organisms introduced to new environments via ship ballast waters. Some phytoplankton species are of particular concern, such as bloom-forming and toxin-producing dinoflagellates (e.g., *Gymnodinium catenatum*), which in addition to vegetative cells have a resting stage (cysts) in their life cycle that favours their transport in the bottom sediment of ballast tanks.

Phytoplankton species, especially those that lead to harmful algal blooms, are regularly monitored by most coastal countries. The tight sampling frequency carried out by each national monitoring program, with the aim of identifying and quantifying the occurrence of toxic phytoplankton in aquaculture-producing areas, has revealed toxigenic phytoplankton species previously known from other geographic ranges (Lewitus et al. 2012). The sudden and abrupt occurrence of algal blooms leads to changes in water quality via two general types of impacts: (1) mechanical or physical damage from high population densities, such as particle irritation or production of a mucous barrier; and (2) chemical effects, such as anoxia or hypoxia, and production of toxins or other metabolites.

The introduction of new toxigenic algae species may modify ecosystem functioning. For example, high levels of emerging and nonregulated toxins can be accumulated by filter-feeding bivalve mollusks, raising new concerns for environmental managers, seafood producers, policy makers, and scientists. The natural development and persistence of algal blooms is controlled by zooplankton grazers and filter-feeding bivalve mollusks. Invasive bivalve mollusk species are often more tolerant to ecosystem changes, and some species seem able to minimise the assimilation of toxins (Burmester et al. 2012), which associated with their high reproduction and growth rates makes them important new resources for fisheries and aquaculture. For these reasons, some bivalve mollusk species have been intentionally introduced. These mollusks easily spread and colonise new ecosystems with devastating ecological effects, such as the decline of native species, changes in community structures, and loss of planktonic productivity, but they can also affect water clarity via alteration of nutrient cycling, organic enrichment of sediment, and transfer of waterborne contaminants to other organisms. Moreover, prolific non-native bivalve species have caused major economic losses, mainly related to activities such as clogging water intake pipes, blocking power plants, damaging irrigation systems, and affecting ship engines (Booy et al. 2017).

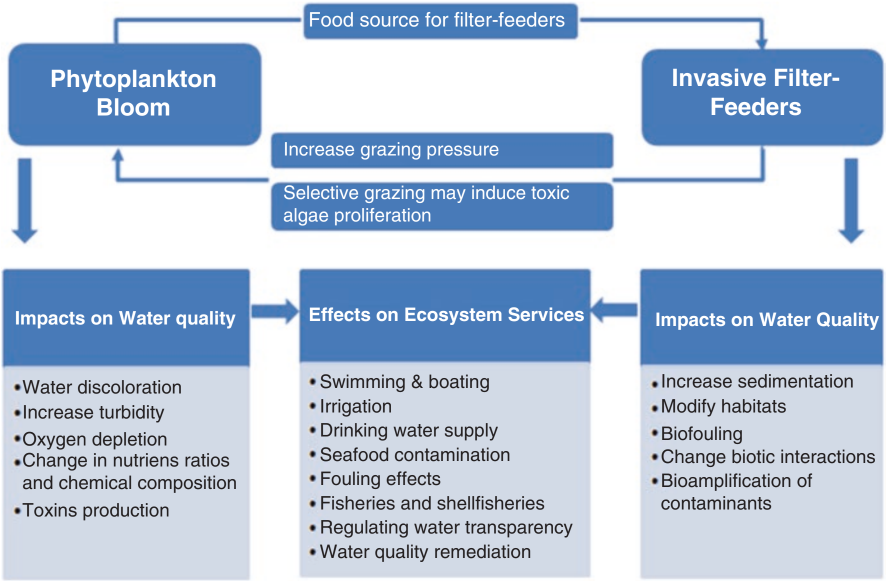

Fig. 14.1 Conceptual diagram of the relationship between phytoplankton blooms and filter-feeding bivalves and derived impacts on water quality and ecosystem services described in other chapters of this book

This chapter describes the impact of selected non-native phytoplankton species and filter-feeding organisms on water quality, with particular emphasis on bivalve mollusks invading marine and freshwater environments, including brackish waters (Fig. 14.1).

14.2 Impacts of Invasive Phytoplankton on Water Quality

Identifying a new phytoplankton species in a given geographic location is often difficult because of the taxonomic complexity of phytoplankton and a lack of comprehensive historical data. The species listed in Table 14.1 are among the most important invasive phytoplankton species known to cause significant ecological and economic impacts in all aquatic system types.

In freshwater, the diatom *Didymosphenia geminata* and the cyanobacteria *Cylindrospermopsis raciborskii* and *Chrysosporum ovalisporum* are key examples of invasive phytoplankton species. *Didymosphenia geminata* is a colonial diatom that has historically been found in the Northern Hemisphere (Whitton et al. 2009). In the past two decades, *D. geminata* blooms have been reported from hundreds of rivers, not only in its native range but also in the Southern Hemisphere. Although somewhat controversial, the situation in New Zealand has gained the most attention where *D. geminata* is extraordinarily prolific because of its probable recent introduction. On the other hand, *Cylindrospermopsis raciborskii* and *Chrysosporum*

Table 14.1 Examples of impacts of invasive bloom-forming phytoplankton species and bivalve mollusks on water quality of freshwater and marine environments

Taxa		Impact	Native area	Introduced area
Freshwater cyanobacteria	*Chrysosporum ovalisporum*	Toxins production (CYN), reduced transparency, water chemical alterations	Middle East	Iberian Peninsula
	Cylindrospermopsis raciborskii	Toxins production (CYN, PSP), reduced transparency, water chemical alterations	America	Europe
Freshwater diatoms	*Didymosphenia geminata*	Sediment covering (extensive thick mats), water chemical alterations	North America, Europe and Asia (North Hemisphere)	New Zealand
Marine dinoflagellates	*Alexandrium minutum*	Toxins production (PSP), water chemical alterations, discoloration of seawater	Egypt (Mediterranean Sea)	Northern Europe, Azores, Australia
	Gymnodinium catenatum	Toxins production (PSP), water chemical alterations	Mexico	Australia
	Ostreopsis cf. *ovata*	Toxins production (PlTX), water chemical alterations, mucous barrier	Thailand	Mediterranean Sea and NE Atlantic
	Prorocentrum minimum	Discoloration of seawater, reduced transparency	Gulf of Lion (NW Mediterranean Sea)	Baltic Sea
Marine diatoms	*Coscinodiscus wailesii*	Gelatinous secretion	NE Pacific, Sea of China and Japan	Europe

(continued)

Table 14.1 (continued)

Taxa		Impact	Native area	Introduced area
Marine bivalves	*Ruditapes philippinarum*	Accumulation of contaminants, nutrient recycling, decrease in turbidity and phytoplankton concentrations, sediment organic enrichment and sedimentation increase	Indo-Pacific	North East Pacific, North East Atlantic, and Mediterranean Sea
	Crassostrea gigas		NW Pacific	North East Pacific, North and South Atlantic, Mediterranean Sea, and Indo-Pacific
Freshwater bivalves	*Corbicula fluminea*	Accumulation of contaminants, nutrient recycling, decrease in turbidity and phytoplankton concentrations, sediment organic enrichment and sedimentation increase, biofouling	SW Asia	Europe, America,
	Dreissena polymorpha		Black, Caspian, Aral, and Azov Seas	Asia, Europe, North America

CYN cylindrospermopsin, *PSP* paralytic shellfish poisoning toxins, *PlTX* palytoxins

ovalisporum are invasive filamentous cyanobacteria that were first assigned to tropical environments, but which, in the past two decades, have spread to subtropical and temperate zones. Both species have the ability to form dormant cells (akinetes) and to fix atmospheric nitrogen, supporting their establishment and proliferation in new environments. *Cylindrospermopsis raciborskii* was first described in Indonesia (Java) in 1912, but in recent years its distribution has spread to almost all continents. It is suggested to have originated in America and then subsequently spread into Africa, followed by movement into Asia and Australia, with Europe being the last continent that it has invaded (Moreira et al. 2015). *Chrysosporum ovalisporum*, previously known as *Aphanizomenon ovalisporum* (Zapomělová et al. 2012), first appeared in Lake Kinneret (Israel) in 1994 as a bloom-forming species and was subsequently described in Australia, Asia, and occasionally in different ecosystems of southern Europe, such as in the Iberian Peninsula (Sukenik et al. 2012).

In marine ecosystems, several diatom and dinoflagellate species have been categorized as invasive. *Coscinodiscus wailesii* is a classic example of an invasive bloom-forming species with harmful effects. This species was originally known from two regions, namely, the northeast Pacific, from California to British Columbia, and the Sea of China and Japanese coastal waters. Extensive detrimental blooms were identified in Europe during the 1970s (Boalch and Harbour 1977), and it has become well established in the North Sea since then. The dinoflagellate *Prorocentrum minimum*, first described in the English Channel, has been increasing in abundance and has spread over large areas. It is now considered the principal invasive phytoplankton species of the Baltic Sea (Olenina et al. 2010). The role of the resting cysts of the toxic marine dinoflagellates *Gymnodinium catenatum* and *Alexandrium* spp. has been pointed out as responsible for their introductions in distinct regions. Although the occurrence of *G. catenatum* on the West Coast of the Iberian Peninsula could result from expansion of its natural range, most likely from northwest Africa (Ribeiro et al. 2012), the presence of *G. catenatum* in Australia suggests a pathway of introduction via ship ballast water, possibly from Japan (Hallegraeff et al. 2012). Finally, it is important to highlight the spread of the tropical and subtropical dinoflagellate genus, *Ostreopsis*, during the past decades throughout the Mediterranean Sea.

14.2.1 Bloom Formation and Collapse

A phytoplankton bloom is intrinsically associated with a significant proliferation of algae cell abundance, often concurrent with a high increase of biomass. Intense blooms commonly result in water discolouration, foul odours and tastes, oxygen depletion, a decrease in water transparency, and other changes in the physical, chemical, and biological parameters of the water bodies.

The most recognised aspect of algal blooms is their propensity to change the water colour. The water of lakes and other freshwater bodies whose surfaces are fully or partially covered by cyanobacteria turns green or greenish. In the marine environment colours of algal blooms are more diverse depending on the type and density of bloom species. Notable changes in water colour and a decline in water transparency were observed after intense blooms (3.5×10^8 cells l^{-1}) of *Prorocentrum minimum* in the Baltic Sea (Olenina et al. 2010). Such high and extensive biomass blooms limit light penetration into the water column, thereby preventing growth of beneficial algae and submerged aquatic vegetation.

The massive blooms of *Ostreopsis* cf. *ovata* in the Mediterranean Sea have been associated with mortality events of benthic communities, including gastropods, bivalve mollusks, cirripeds, cephalopods, echinoderms, and fishes. Morphological anomalies, loss of substrate-adhering capacity, and other damage were also registered in the affected organism. *Ostreopsis* are aggregated in mucilage that increases during cell proliferation, giving *Ostreopsis* the ability to rapidly colonize benthic substrates. It has been pointed out that the mucilage matrix plays a role in bloom toxicity by actively disseminating the toxins, as affected benthic organisms are often covered by it (Giussani et al. 2015). Extensive mucilage production is also associated with blooms of the giant diatom *Coscinodiscus wailesii* (Boalch and

Harbour 1977). The grayish mucilage is described as a highly sticky material, containing plankton remains and other solid particles, which impairs fishing nets and trawling activities. The mucilage formation seems to be related to cell lysis and bloom senescence, which may influence the biogeochemical cycles of regions where intensive blooms occur. In oligotrophic systems, *Didymosphenia geminata* often forms nuisance blooms consisting of thick mats that cover great extents of the bottom of streams and rivers. These mats may lead to changes in the composition and abundance of benthic invertebrates that can occur as a result of alterations in several mechanisms, including physical habitat and water chemistry. The presence of *D. geminata* mats promotes changes in hydrodynamic conditions by covering exposed sediment and increasing diurnal fluctuations in pH and dissolved oxygen (Larned and Kilroy 2014).

Extensive blooms consume nutrients, and thus may affect the water nutrient pools and dynamics. Algal blooms may occur at both extremes of the nutrient gradient, either in oligotrophic or nutrient-enhanced habitats. The nutrient uptake kinetics of phytoplankton species are affected by many processes, such as luxury consumption, local inputs, and transient nutrient pulses, which means that patterns between algal bloom development and external nutrient concentration are not generally clear and may be interpreted in different ways (Vila et al. 2005). When high biomass blooms exceed the assimilative capacity of the system, anoxia occurs. Oxygen depletion in the water column may result from intense algal respiration and incomplete phytoplankton decomposition at the bottom.

14.2.2 Toxin Production

One of the most significant impacts posed by bloom-forming invasive phytoplankton species on water quality is their potential for the production of toxic secondary metabolites, which leads to adverse health effects on plants and animals. These compounds vary from small to complex molecules (mol. wt. > 2600 Da). Their mode of action in mammals (the main organism models studied) includes inhibition of sodium channels, blocking neuromuscular transmission, and inhibition of protein phosphatases, leading to neuro- and hepatotoxic effects. The toxins can be released into the water or incorporated by the biota via food web transfer, resulting in different routes of exposure: drinking water, seafood contamination, aerosols, etc.

The marine dinoflagellates *Gymnodinium catenatum* and *Alexandrium* spp. are responsible for paralytic shellfish poisoning (PSP) outbreaks reported throughout the world's coastal regions. PSP is considered the most widespread of the algal blooms-related shellfish poisoning syndromes, as PSP toxins are potent neurotoxins that may cause human fatalities. The impacts of these toxin-producing dinoflagellates can be devastating for shellfish industry because of long-term closures of harvesting, and increasing geographic distribution and frequency of blooms of toxic *Alexandrium* populations have been reported. A recent example is the first report of a massive bloom (1.3×10^7 cells l^{-1}) of *A. minutum* in a remote coastal lagoon in São

Fig. 14.2 The first bloom of *Alexandrium minutum* in the Azores (Santo Cristo Lagoon, S. Jorge Island, Portugal) in September 2013 (Photograph by Rui Sequeira)

Jorge Island in the Azores in late 2013 (Santos et al. 2014). This island, located in the middle of the North Atlantic Ocean at a distance of 1500 km from the African/European coast, is surrounded by oligotrophic waters with low phytoplankton biomass. The bloom caused an orange-brown water discolouration (Fig. 14.2), culminating with the death of small pelagic fish, toxification of shellfish resources, and human poisonings after consumption of shellfish. Extremely high levels of PSP toxins that exceeded the Regulatory Limit (800 μg STX equiv. kg^{-1}) by more than 30 fold were determined in shellfish, which lead the local authorities to ban shellfish harvesting for more than 6 months.

The Mediterranean Sea marine region has the most non-native species in Europe (Vilà et al. 2010). Of increased concern is the impact of the benthic and epiphytic dinoflagellate genus, *Ostreopsis*, particularly *O.* cf. *ovata*, which produces palytoxin or palytoxin-like compounds (ovatoxins). Acute symptoms, including high fever, watery rhinorrhea, pharyngeal pain, bronchoconstriction with mild dyspnea and wheezes, conjunctivitis, and dermatitis, were observed in people exposed to seawater on Mediterranean beaches. The symptoms were severe at the peak of the bloom and dissipated with their senescence. This coincidence suggested that *Ostreopsis* cells or their toxins were transferred into the air through a mechanism similar to that previously observed with brevetoxins and microcystins in the Gulf of Mexico and in Californian lakes, respectively. However, it was only recently that the presence of ovatoxins was successfully determined in marine aerosols by high resolution mass spectrometry (Ciminiello et al. 2014). Figure 14.3 illustrates the spread of *Ostreopsis* throughout the Mediterranean Sea since its first toxic outbreak in 1998 until its detection on the Atlantic coast of Morocco, the Canary Islands and Portugal. Some countries (e.g., Italy and France) that frequently experience *Ostreopsis*-related outbreaks have developed close collaborations between policy makers and scientists to take management actions against these algal blooms.

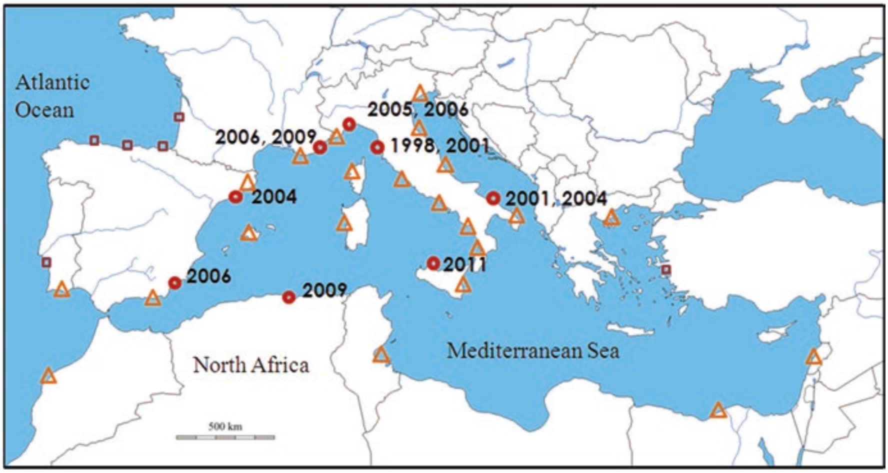

Fig. 14.3 Spread of *Ostreopsis* spp. in the Mediterranean Sea and the Atlantic coast. *Circles* indicate where and when human health outbreaks associated with *Ostreopsis* blooms occurred; *triangles* indicate where blooms have been detected; *small rectangles* indicate locations where *Ostreopsis* cells have been observed (Adapted from Ciminiello et al. 2014)

The invasive filamentous diazotrophic cyanobacteria *Cylindrospermopsis raciborskii* and *Chrysosporum ovalisporum* are a major concern regarding freshwater water quality. Some *C. raciborskii* toxic strains in South America have been reported to produce PSP toxins. However, many of the toxic strains of *C. raciborskii* and *C. ovalisporum* have been found to produce cylindrospermopsin (CYN). This alkaloid is a cytotoxin that can cause human poisoning. An outbreak of hepatoenteritis affecting 148 people, mostly children, was first reported in 1979 on Palm Island (Queensland, Australia) as a result of the consumption of water contaminated with CYN produced by *C. raciborskii* (Griffiths and Saker 2003). In addition to the human diseases reported here, aquatic toxins also cause devastating effects on benthic and pelagic communities. Bioaccumulation of toxins produced by freshwater cyanobacteria, such as CYN, has been documented in a range of aquatic vertebrates and invertebrates potentially affecting higher trophic levels. Bottom-up effects may also result from domination of nuisance cyanobacteria through alteration of the zooplankton community. The presence of toxin-producing *C. raciborskii* in the St. Johns River System (Florida) promoted a decrease in the size structure of the zooplankton community, pointing to an inevitable decline in the carbon and energy transfer efficiency to higher consumers (i.e., fish) (Leonard and Paerl 2005). Mass development of *G. catenatum* and *Alexandrium* spp. blooms and trophic transfer of PSP toxins has resulted in mass mortality of fish and other marine organisms, including top predators such as seabirds and sea mammals (Costa 2016).

14.3 Impacts of Invasive Freshwater and Marine Filter Feeders on Water Quality

Filter-feeding bivalves play a relevant role in ecosystems functioning by influencing the primary productivity through strong top-down control on phytoplankton. By filtering suspended particles from the water column and sinking these into the sediment surface as faeces and pseudofaeces, bivalves also have a role in nutrients dynamics. Additionally, bivalves are an important food source for higher trophic levels, which makes them an entry point for toxins through the food webs. All these processes may be exacerbated by invasive bivalve species leading to significant impacts on water quality.

Tremendous ecological and economic impacts have been promoted by invasive freshwater bivalve species (Gutierrez 2017). The zebra mussel, *Dreissena polymorpha*, and the Asian clam, *Corbicula fluminea*, have been responsible for the highest number of documented cases (Sousa et al. 2014). *Corbicula fluminea* is a freshwater clam native to Asia, which, over the past century, has spread its distribution to several continents including America (North and South) and Europe. *Dreissena polymorpha* is native to fresh and brackish waters of the Ponto-Caspian basins, revealing its strong invasive character first in Europe and later in North America.

The Manila clam, *Ruditapes philippinarum*, is native to the Indo-Pacific region. It has been introduced worldwide, mostly for cultivation purposes. It was accidentally introduced during the 1930s to the Pacific Coast of North America along with the Pacific oyster, *Crassostrea gigas*, seed imports, and has naturally spread to the Pacific Coast from California to British Columbia. It was also introduced into France in the early 1980s and since then in several other European countries to compensate for the irregular yields of the native European congeneric species *Ruditapes decussatus* (Bidegain and Juanes 2013). Other important species that have been introduced for cultivation purposes worldwide include the oysters *C. gigas*, *C. ariakensis*, *C. virginica*, and *Ostrea edulis*; the hard clam, *Mercenaria mercenaria*; and the softshell clam, *Mya arenaria.*

14.3.1 Water Clearance Effects

Invasive bivalves, such as the zebra mussel, the Asian clam, and the Manila clam, may significantly increase the grazing pressure in aquatic systems with consequent top-down control effects. A classical example is that of the massive decline in phytoplankton biomass (85 %) concurrent with the invasion of zebra mussels in the Hudson River Estuary (Caraco et al. 1997). In addition to the grazing pressure promoted by the invasive bivalve species, selective ingestion of particles dictated by the characteristics of the bivalve mantle cavity, selective digestion of phytoplankton, and selective removal of less buoyant and slower growing phytoplankton species may lead to drastic changes in phytoplankton composition. For these reasons, the presence of invasive bivalves (e.g., *D. polymorpha*) has been often associated with changes in cyanobacteria dominance and the promotion of toxic groups, namely *Microcystis* (Vanderploeg et al. 2001).

Under turbid conditions, some of these invasive species increase the rate of particle removal, improving water clarity and thereby enhancing benthic macroalgal or eelgrass production. The establishment of a *Dreissena polymorpha* community in Lough Sheelin, Ireland, and its increased population in the following years resulted in shellfish populations capable of filtering the total volume of the lake (82×10^6 m^3) within 13 days (Millane et al. 2008). The macrobenthic filtration capacity in the Venice lagoon more than doubled with the introduction of *R. philippinarum* (the Manila clam) (Pranovi et al. 2006). The increase in water clarity through the active filter-feeding behaviour of invasive bivalves might be used as support for a misconception that bivalve introductions lead to significant improvements in water quality. Nevertheless, high clearance rates also alter nutrient cycling (i.e., increase concentrations of ammonia, nitrates, and phosphates) and increase deposition of ingested particles as faeces and pseudofaeces adding organic matter to sediments (Sousa et al. 2014).

Invasive bivalves, such as *C. fluminea*, trap metal contaminants and accumulate them. This trait might be considered as an ecosystem service when these bivalves are used for bioremediation of metal-bearing effluents (Rosa et al. 2014). However, metal accumulation by invasive bivalves is likely to become biomagnified along the food chain with important impacts on higher trophic levels, as was verified in San Francisco Bay, where *Corbula amurensis* was observed to trap selenium and the effects of this metal were biomagnified along the food chain (Stewart et al. 2004).

14.4 Ecological Side Effects of Bivalve Mollusk Culture and Harvesting

Many non-native bivalve species have been deliberately introduced for aquaculture purposes or to improve fisheries yield. Harvesting devices vary in their design and implementation, but mechanical and hydraulic shellfish dredges are some of those most used for species with high economic value (Fig. 14.4). The action of mechanical and hydraulic shellfish dredges physically disrupts the benthic substrate and may suspend sediment, increase turbidity, alter substrate composition, and cause sediment plumes. The resuspension process of contaminated sediments (e.g., metals, tributyltins, polycyclic aromatic hydrocarbons, polychlorinated biphenyls, and pesticides) releases contaminants into the surrounding water column that may then become biologically available (Eggleton and Thomas 2004).

Other faunal activities of introduced non-native species include burrowing, ingestion and defecation of sediment grains, and consumption of the vegetation. In special circumstances, the benthic infauna influences the distribution of oxygen in sediments through active mixing of sediment particles (i.e., bioturbation). These

Fig. 14.4 Harvesting of the Manila clam, *Ruditapes philippinarum*, with shellfish dredges in the Tagus estuary, Portugal (Photograph by Paula Chainho)

activities also intensify the benthic–pelagic coupling because benthic infauna can profoundly influence N cycling through their feeding, metabolic, burrow construction, bioturbation, and sediment ventilation activities (Welsh 2003).

14.5 Conclusions

Many phytoplankton species are transported by ship ballast waters. Some of these species, when introduced, form phytoplankton blooms with severe impacts on water quality. The occurrence of harmful algae species in regions where they were not previously observed has lead to a vast array of different impacts, including the production of an uncharacterised suite of toxic compounds, depletion of oxygen, production of mucilage covering benthic communities, decreased water transparency, water discolouration, and foul odours and taste. Filter-feeding bivalve mollusks have a key role controlling the proliferations of these harmful algae. The filtering capability by native and non-native bivalve species may cause massive declines in phytoplankton biomass, mitigating the effects of algal proliferations. The high abundance of invasive bivalves can also promote the filtration of large volumes of water, removing suspended particles and thus increasing the transparency of certain aquatic systems. Nevertheless, the high densities and high biomass achieved by invasive bivalve species can cause considerable ecological problems and physical environment modifications via selective grazing of phytoplankton species that induce the dominance of toxic groups, altering nutrient dynamics, increasing sedimentation, biofouling, changing biotic interactions, and enabling the accumulation and transfer of contaminants. Understanding the impacts of invasive species on water quality is crucial for supporting further legal water framework directives and environmental management decisions.

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Chapter 15
Impact of Biological Invasions on Infrastructure

Olaf Booy, Lucy Cornwell, Dave Parrott, Mike Sutton-Croft, and Frances Williams

Abstract Non-native species cause significant damage to hard infrastructure across the globe, affecting buildings, transportation, water and energy supplies. This review provides a broad account of non-native species impacts on infrastructure with links, directly or indirectly, to ecosystem services where relevant. The impacts of non-native species on hard infrastructure are discussed, with examples taken from around the world of some of the most prominent impacts. Of the non-native species listed as among the world's worst 100 species by the IUCN, 14 are recognised as having impacts on hard infrastructure, with damage to buildings being most common (9 species) followed by energy and water (7 species each) and finally transport (5 species). Several species affect more than one infrastructure type, particularly for water and hydroelectric energy infrastructure. Using Great Britain as a case study, the economic costs arising from infrastructure impacts by non-native species are reviewed. Overall, a conservative estimate of the direct cost of non-native species to infrastructure in 2010 was approximately £310 million per annum, comprising 18 % of the overall cost of non-native species to Great Britain (£1.7billion).

Keywords Buildings • Economic impact • Energy • Fouling • Structural damage • Transport • Water

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15.1 Introduction

Infrastructure is the fundamental network necessary for an economy to function effectively and includes technical structures such as roads, bridges, viaducts, tunnels, water supply, sewerage systems, electrical grids, and telecommunications. It has often been a major cause of non-native species introduction and spread around the world (Essl et al. 2015); for example, road and rail facilitating the spread of terrestrial non-native species, canals linking previously isolated water catchments and oceans (Zenetos et al. 2012) and built infrastructure facilitating the spread of non-native species in the marine environment (Airoldi et al. 2015). However, these structures are also vulnerable to the impacts of non-native species, which can cause structural failures, impede their use, and disrupt important services.

Infrastructure tends to be a high-cost investment and a major enabling component of any economy. Thus, impacts arising from non-native species on infrastructure can have major consequences on human well-being, because the affected infrastructure often provides commodities and services essential to enable, sustain, or enhance societal living conditions. Here, we examine the impact of non-native species on four broad categories of hard infrastructure that represent large physical networks necessary for the functioning of a modern industrial nation: building, transport, water, and energy.

15.2 Damage to Buildings

Non-native species have numerous impacts on buildings and the services on which they depend, including directly damaging construction materials, such as wood or plastic, and indirectly damaging structures, for example as a result of increased flooding or fire risk. Non-native species invading households can also cause infestations that reduce or prevent the use of the buildings.

Invasive termites are reported to cause some of the most significant direct damage to buildings, with 28 invasive species known worldwide. The Formosan subterranean termite, *Coptotermes formosanus*, was introduced to the USA from eastern Asia, probably in crates used to transport military equipment after World War II. The species now costs more than US$1 billion per annum in prevention, treatment, and repair costs (Lax and Osbrink 2003), as well as causing damage to other infrastructures such as communications (telephone poles and cables) and energy (electrical cables). Japanese knotweed, *Fallopia japonica*, also provides an unusually expensive example of the impact invasive weeds can have on built infrastructure. In Great Britain alone, the cost of this species to homeowners and developers, as a result of damage, management costs, and reduction in house prices, was estimated to be £160 million per annum in 2010 (Williams et al. 2010) (Table 15.1).

In areas where wildfires are common, invasive plants, such as buffel grass, *Cenchrus ciliaris*; cheat grass, *Bromus tectorum*; and tamarisk *Tamarix* spp. can impact fire regimes by increasing biomass and flammability and changing the distribution of flammable material. If these fires spread to residential areas, they can cause serious damage.

Infestations of rodents and insect pests, such as cockroaches, can be a significant problem in homes and other infrastructure where they cause a nuisance, contaminate food, and spread disease. In the United States alone, at least US$1 billion is spent each year on the control of cockroaches (Rust 2008), including the German cockroach, *Blattella germanica* (native to southeast Asia); the American cockroach *Periplaneta Americana* (native to tropical Africa), and the Oriental cockroach, *Blatta orientalis* (native to North Africa).

15.3 Damage to Transport Infrastructure

Non-native species affect many forms of transport infrastructure including roads, rail, canal networks, ports, and harbours. Road and rail networks are directly affected by invasive plants, which can grow through surfaces, and invasive animals, which may burrow into or underneath supporting structures (Booy et al. 2008). Non-native species are also managed to prevent overgrowth restricting the vision of drivers (e.g., catclaw mimosa, *Mimosa pigra*, and buddleia, *Buddleja davidii*); reduce delays caused by vegetation on railway lines (e.g., kudzu, *Pueraria montana* var. *lobata*); and to prevent direct health risks to workers (e.g., oak processionary moth, *Thaumetopoea processionea*). Aquatic plants can block canals, restricting access and navigation (e.g., hydrilla, *Hydrilla verticillata* and Eurasian watermilfoil, *Myriophyllum spicatum*, in the USA), in addition to structural damage caused by invasive riparian plants and burrowing animals on the banks of water bodies. Water hyacinth, *Eichhornia crassipes* is an infamous example of an invasive non-native species that grows in such dense mats that it can hinder transport along canals and other water bodies (see Case Study 1, Sect. 15.4.1; Fig. 15.1) and has “paralysed activities in ports, villages and bays” in Africa (Julien et al. 2006). Similarly, giant *Salvinia molesta* is a severe problem in some tropical and warm temperate regions of the world, where it has severely affected communities that rely on waterways for transport (McFarland et al. 2004).

In the marine environment, infrastructure impacts are caused by biofouling in marinas, ports, and harbours. Direct damage is reported in some cases, for example, where mollusk block water intakes of associated facilities, as are aesthetic impacts, where fouling of wharf pilings, jetties, and ropes can become unsightly (e.g., dead man’s fingers, *Codium fragile* ssp. *tomentosoides*, in Australia). The non-native seaweeds *Sargassum muticum* and *Undaria pinnatifida* are regarded as navigational hazards along many of the Venice lagoon canals as they alter the seabed and canal landscape and entangle boats (Streftaris and Zenetos 2006). Other in-water structures associated with transport may also be affected, such as the fouling of navigation buoys. Prolific fouling by non-native species may increase maintenance costs in marinas, ports, and harbours, although this is rarely reported and appears not to be an economic concern in Great Britain (Williams et al. 2010; Table 15.1) despite the invasion of numerous marine biofouling species. Fouling/clogging is also a problem with mass swarms of the jellyfish *Rhopilema nomadica* that are reported along the Levantine coast and as far north as the southeastern coast of Turkey, where they are reported to have clogged coastal installations (Streftaris and Zenetos 2006). Perhaps the most significant cost is associated with the management of non-native species to prevent fouling of boats and reduce spread from marinas, ports, and harbours. For example, in excess of AUS$2.2 million was spent to eradicate the marine black striped mussel *Mytilopsis sallei* from marinas in northern Australia (Bax et al. 2002).

15.4 Damage to Water Infrastructure

Water infrastructure for municipal and agricultural purposes includes channels, pipes, reservoirs, pumps, and facilities that use and treat raw water. Important to the efficient running of these services are water flow, water purity, and the maintenance of structures and equipment used in the water, all of which can be affected by non-native species (Catford 2017). Some of the most expensive impacts are caused by the zebra mussel, *Dreissena polymorpha*, a prolific biofouling agent that blocks pipes and screens and causes maintenance issues costing water-using industries in Europe and North America billions of dollars (Aldridge et al. 2004). Similar issues are caused by other invertebrates (e.g., the Asian clam, *Corbicula fluminea* and the quagga mussel, *Dreissena bugensis*) as well as invasive weeds (e.g., curly waterweed, *Lagarosiphon major* and water hyacinth, refer to Case Study 1, Sect. 15.4.1). In some cases, non-native species can cause direct physical damage to water infrastructure such as levees, dykes, and reservoirs, for example, as a result of burrowing by the red-swamp crayfish, *Procambarus clarkii* (Holdich 1999) and the Chinese mitten crab, *Eriocheir sinensis* (Streftaris and Zenetos 2006). Vertebrates are also capable of causing damage, for example, the South American coypu, *Myocastor coypus*, which damages the banks of waterways and dykes (McLaughlan et al. 2014).

15.4.1 Case Study 1: Infrastructure Impacts of Water Hyacinth

Water hyacinth, *Eichhornia crassipes*, is one of the most damaging freshwater aquatic plants worldwide and is particularly problematic in Africa. Lake Victoria, the world's second largest freshwater lake, spans three African countries providing drinking water, food, energy, and tourism to support an estimated 25 million people. In 1989, water hyacinth was discovered in the Ugandan and Tanzanian areas of the lake, and in the Kenyan section the following year. At its peak, the mat of vegetation covering Lake Victoria was estimated to be growing at 3 hectares per day, impacting heavily on normal use of the lake including the generation of hydroelectric power (Ayodo and Jagero 2012). In Kisumu, Kenya, pipes supplying water to local communities were restricted by debris, reportedly halving the volume of water available from 20,000 m^3 to 10,000 m^3 per day in 2001 (Julien et al. 2006). The thick mats created by water hyacinth also affect navigation and water supply, for example, in Port Bell in Uganda, where ships attempting to dock struggle to pass through the dense vegetation. In Uganda, turbines at the Owen Falls dam were frequently clogged by mats of water hyacinth, and had to be turned off to allow water hyacinth debris to be cleared from the screens (Julien et al. 2006). Water hyacinth also blocks waterways in many other areas of its invasive range, including Central America, southern USA, other parts of Africa, southeast Asia, and Australia. In Mexico more than 40,000 ha of dams, lakes, canals, and drains are infested (Gutierrez et al. 1996), and US$12 million per year is spent in China to control water hyacinth and maintain navigation through canals (Julien et al. 2006).

Fig. 15.1 Water hyacinth, *Eichhornia crassipes*, can have heavy impacts on water, energy, and transport infrastructure, as in this case where its prolific growth is blocking the navigation of a canal (Photograph by Arne Witt, CABI)

15.5 Damage to Energy Infrastructure

Power production facilities require large volumes of water for cooling, usually taken from large water bodies where non-native species can present a biofouling hazard. The Asian clam *C. fluminea* is a significant biofouler of power plants in the USA, where juvenile clams infiltrate and clog cooling and condensing systems. Operations at numerous power stations, including nuclear power stations, have been affected with downtime, corrective actions, and maintenance costing billions of dollars (OTA 1993). Similar problems have been caused by other mollusks (e.g., zebra and quagga mussel), jellyfish, and plants (e.g., water hyacinth in hydroelectric power plants, see Case Study 1, Sect. 15.4.1).

Power lines, pylons, and domestic electrical wiring can also be vulnerable to damage. For example, the brown tree hyacinth, *Eichhornia crassipes*, was accidentally introduced from its native range in the South Pacific to Guam shortly after World War II and has been responsible for thousands of power outages. These snakes climb power lines, and enter transformers and electrical boxes and cause outages, which occur on average once every 2–3 days, costing an estimated US$1–4 million per annum in direct damage and loss of productivity (Fritts 2002). Similar impacts are caused by the highly invasive vine *Pueraria montana* var. *lobata* which smothers poles and lines, costing US power companies an estimated US$1.5 million per year (Blaustein 2001), and the monk parakeet, *Myiopsitta monachus*, whose nests can cause outages, electrical fires, and safety issues (see Case Study 2, Sect. 15.5.1).

15.5.1 Case Study 2: Monk Parakeets and Electrical Utility Structures

The monk parakeet, *Myiopsitta monachus*, originates from South America, and is unique amongst psittacines in that it builds stick nests, rather than occupying secondary cavities. Nests can measure 1 m or greater in diameter and are regularly built on man-made structures (Fig. 15.2). This predilection has proven to be a particular problem in the United States where, in some locations, 80 % of monk parakeet nests occur on such structures, including electrical utility structures such as transmission lines, substations, and distribution lines (Newman et al. 2008).

The parakeets' habit of nesting on electrical utility structures causes significant problems with electrical reliability (Newman et al. 2008). Nest material can cause short circuits and electrical fires resulting in damage and power outages and an increase in operation and maintenance costs associated with nest removal and repair. In South Florida, an economic analysis estimated nest removal costs of US$415–1500 per nest and, over a 5-year period, nest removal alone was estimated to have cost between US$1.3–4.7 million (Avery et al. 2008).

Fig. 15.2 Monk parakeet, *Myiopsitta monachus*, nesting on a mobile phone mast in the UK (Photograph by Olaf Booy, Non-native Species Secretariat)

In addition, a number of safety concerns have been identified, including putting those who rely on a continuous power supply at risk (e.g., people on life support systems); exposing maintenance crews to allergenic material associated with nests (including nest mites); and incentivising trespassers attempting to trap monk parakeets to sell in the pet trade to enter substations where they have been electrocuted (Newman et al. 2008).

15.6 Cost of Non-native Species to Infrastructure in Great Britain

A comprehensive assessment of the economic impact of invasive non-native species in Great Britain (Williams et al. 2010) allows for an overview of the cost of infrastructure impacts at a national scale (Table 15.2). Although Williams et al. (2010) provide a specific cost for infrastructure, this was a narrow definition limited to buildings and has been expanded here to include transport networks and relevant aspects of water and energy infrastructure. In total, a conservative estimate of the

Table 15.1 Economic costs associated with non-native species infrastructure impact in Great Britain

Infrastructure	Damage	Example species	Estimated annual cost
Buildings	Mitigation and delay costs to development	*Fallopia japonica*, *Buddleja davidii*, other non-native plants	£152,256,000
	Damage to and maintenance of properties	*Fallopia japonica, Glis glis, Sciurus carolinensis, Psittacula krameri, Reticulitermes grassei*	£8,237,000
	Property devaluation	*Fallopia japonica*	£1,116,000
	Infestation	*Rattus norwegicus, Mus musculus, Blatta orientalis, Blattela germanica*	£87,673,840
	Damage to listed buildings	*Buddleja davidii*	£612,000
Transport	Road damage and mitigation	*Oryctolagus cuniculus, Fallopia japonica*, and other non-native plants	£6,752,887
	Road vehicle collisions and culling	Non-native deer	£10,266,704
	Canals and river navigation damage, mitigation and vegetation management	*Pacifastacus leniusculus, Eriocheir sinensis, Dreissena polymorpha*, and non-native vegetation	£1,850,000
	Railway damage and mitigation	Non-native trees and plants	£25,400,000
	Railway delay and repair	*Rattus norvegicus*	£5,060,000
Water	Water industry: need for maintenance and modification	*Dreissena polymorpha* and other non-native species	£1,443,259
Energy	Power production facilities: need for maintenance	*Lagarosiphon major, Eriocheir sinensis, Dreissena polymorpha*, and other non-native species	£523,000
	Power company maintenance and repair to power lines	Non-native trees	£200,000

Source*:* Data from Williams et al. (2010)

direct cost of non-native species to infrastructure in 2010 was approximately £300 million per annum, making up 18 % of the overall cost of non-native species to Great Britain (£1.7 billion). Costs associated with construction and the upkeep of buildings accounts for the majority of overall infrastructure costs, almost £250 million (80 % of the total infrastructure costs), largely because of Japanese knotweed, *Fallopia japonica*, but also caused by infestation by rats, mice, and cockroaches. Transport costs account for 16 % of the total (approximately £49 million), with rail the most expensive, largely as a result of the need for vegetation management, but also because of damage and delays caused by fallen trees, leaves on the line, and rats chewing through equipment and cables. Deer vehicle collisions are a substantial cost associated with road transport infrastructure; while costs associated with other forms of transport such as canals and navigable rivers are relatively small. Although shipping and hull fouling costs are reported in the marine environment, no costs are given for maintaining infrastructure associated with marinas, ports, and harbours. Infrastructures associated with water and energy have suffered relatively small costs as a result of non-native species in Great Britain, mostly as a result of invasion by aquatic species but also from non-native trees bringing down power lines.

15.7 Infrastructure Impacts of 100 of the World's Worst Non-Native Species

An indication of the significance of non-native species infrastructure impact at a global scale can be explored using the IUCN list of '100 of the world's worst' (Lowe et al. 2000). The 'impact' entry for each of these species on the Global Invasive Species Database (http://www.issg.org/database/welcome) was reviewed for reference to infrastructure impact and results categorised by sector (Table 15.2). The results show that 14 of the listed species have significant impacts on infrastructure, with damage to buildings being most common (9 species), although fewer species affect other forms of infrastructure; for example, 7 species affect energy and water, and 5 species affect transport. Ten of the listed species recorded as having an impact on infrastructure occupied primarily terrestrial habitats; only 4 were primarily freshwater and none was primarily marine.

Table 15.2 Infrastructure impacts described for the IUCN world's worst non-native species

Species	Buildings	Transport	Water	Energy	Infrastructure impacts cited in the GISD
Acacia mearnsii			X		Notable primarily for its environmental impacts, but also causes damage to infrastructure as a result of riverbank erosion in South Africa, as well as other African countries and the USA (Rowntree 1991).
Arundo donax	X		X		Invasive in many countries where dense populations in river channels increase flood risk and riverbank erosion (Spencer et al. 2013). Can cause blockages and structural damage (e.g., to culverts, bridges). Extremely flammable, increasing the likelihood and intensity of fires that which are often near urban areas (Giessow et al. 2011).

(continued)

Table 15.2 (continued)

Species	Buildings	Transport	Water	Energy	Infrastructure impacts cited in the GISD
Boiga irregularis				X	Causes power outages which are a serious problem on Guam resulting in thousands of power outages and costs conservatively estimated at $1–4 million dollars each year (Fritts 2002)
Coptotermes formosanus	X			X	Feeds on wood, damaging buildings, communications, and energy cables. Costs over US $1 billion per annum in the USA (Lax and Osbrink 2003).
Dreissena polymorpha			X	X	A significant biofouling agent of pipes, intakes, and other parts in water structures estimated to cost > $1billion per annum in the US and Europe (Aldridge et al. 2004).
Eichhornia crassipes	X	X	X	X	Causes significant problems worldwide by increasing flood risk, preventing transport, slowing water flow and water intake, and damaging canal banks (Julien et al. 2006).
Eriocheir sinensis		X	X		Damages levees and stream banks by burrowing behaviour, interfering with water provision; can damage canal banks (Kateregga and Sterner 2006).
Fallopia japonica	X	X			Grows through and damages buildings, roads, and other structures. Invasive in Europe and North America, with cost in Britain estimated to be £160 million per annum (Williams et al. 2010).
Mimosa pigra	X	X		X	Reduces water flow, threatening sustainability of reservoirs and canals. Reduces access to electricity poles and cables. In Thailand, grows rapidly along national highways, decreasing the visibility of drivers and increasing the potential for traffic accidents.
Myocastor coypus	X		X		Burrowing behaviour undermines river banks and dykes, increasing the threat of flooding (McLaughlan et al. 2014).
Pueraria montana var. *lobata*	X			X	Significant problem in the USA where rapid growth overgrows buildings, amenity planting, roads, and railways. Can smother power cables and pylons, costing $millions each year (Blaustein 2001).

(continued)

Table 15.2 (continued)

Species	Buildings	Transport	Water	Energy	Infrastructure impacts cited in the GISD
Salvinia molesta		X	X	X	Significant invader in many parts of the world where thick mats prevent passage of boats, impede transport, reduce access to water, and block intakes of hydroelectric plants (McFarland et al. 2004).
Sturnus vulgaris	X				Can be a nuisance in buildings, causing damage to roof linings and fouling in roof cavities.
Sus scrofa	X				Rooting and grubbing behaviour causes a wide range of impacts, including damage to property and green landscaping (for example, damage to ornamental plantings, turf, and golf courses).

See http://www.issg.org/database for details

15.8 Conclusions

Several non-native species have been introduced for their beneficial effects on infrastructure; for example, some non-native species help to stabilise land and reduce erosion, preventing damage. However, non-native species generally have considerable and wide-ranging impacts on infrastructure, particularly affecting buildings, transport, water, and energy infrastructures. The scale of impact is illustrated at a national level by figures from Great Britain, which incurs infrastructure costs of more than £300 million per annum, representing 18 % of the total cost of non-native species to the economy. At a global level, 14 of the 100 non-native species considered to be among the worst in the world are listed, at least in part, because of significant infrastructure impacts. Damage to buildings is a major component of infrastructure impact, which is reflected both in the costs for Great Britain and for the IUCN 100 ‘worst’ non-native species list, but costs to other types of infrastructure are also considerable (e.g., US$ billions to power plants and water treatment).

Although non-native species can directly impact infrastructure (e.g., damage inflicted by termites on buildings or Japanese knotweed growing through road surfaces), they can also cause indirect impacts by modifying ecosystems. For example, hard infrastructure benefits from regulating ecosystem services that provide flood alleviation. Non-native species can undermine this service by blocking channels, increasing erosion, and undermining flood defences, putting infrastructure at risk. Similarly, natural fire regimes can be altered by non-native species causing significant damage to infrastructure. Non-native species may also damage or restrict the ability of infrastructure to deliver services derived from ecosystems, such as the provision of good water quality through reservoirs, canals, pipes, and other in-water structures. Cultural services provided by ecosystems associated with infrastructure can also be negatively affected, such as in waterbodies invaded by macrophytes that prevent navigation.

The impacts of non-native species on infrastructure, and the risk that the infrastructure itself can spread non-native species, has led to sector-specific guidance for infrastructure managers (e.g., Wittenberg and Cock 2001; Booy et al. 2008; IPIECA 2010; Airoldi et al. 2015). Given the costly and global nature of this problem, more mechanisms are required to further develop and share such good management practice.

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Chapter 16
Alterations of Disturbance Regimes by Plant and Animal Invaders

Mirijam Gaertner, David C. Le Maitre, and Karen J. Esler

Abstract Disturbances, or changes in disturbance regimes, can promote invasions, but invasives can also be seen as drivers of disturbances. Non-native species can either change an existing disturbance regime or introduce disturbance regimes that are novel to the invaded system. Changes in disturbance regimes can be triggered if non-natives act as biotic disturbance agents, if non-natives interact with physical forces of disturbance, or by the introduction of novel functional traits. Reinforcing feedback loops between the disturbance and the non-native species often promote the non-native species to the disadvantage of the native species, which can result in losses of biodiversity, altered ecosystem functioning, and a changed capacity to provide ecosystem services. Changes in disturbance regimes because of invasions and the resulting ecological impacts are well established. However, the effects of changed disturbance regimes on regulating ecosystem services have so far received little attention. This chapter describes the key aspects of disturbance regimes that can be altered by invasions and gives examples of different types of regulating ecosystem services affected by these alterations. The chapter focuses on terrestrial ecosystems, covering a wide range of different taxa.

Keywords Carbon sequestration • Disturbance • Ecological impacts • Feedback loops • Fire regimes • Water flow regulation • Wild boar

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16.1 Introduction

Biological invasions can alter disturbance regimes beyond the range of variation to which native species are adapted, resulting in community changes and ecosystem transformations (Brooks et al. 2004). Disturbances have been defined as being "relatively discrete events in time that disrupt population, community and ecosystem structures and bring about a change in resources, substrate availability or the physical environments" (White and Pickett 1985). Following Sher and Hyatt (1999), we refine this definition for invasion-mediated disturbances. Invasion-mediated disturbances can bring about a change in historical disturbance regimes, altering the rate or intensity of the resource flux in a habitat. Such resources can include space, nutrients, water, or light. Ecosystems adapt to disturbance regimes rather than to disturbance per se, and the regimes are typically characterised by distributions of a number of key characteristics: frequencies or recurrence intervals; intensity or severity; duration; extent; rate of change; and sequences of disturbances (Miller et al. 2011). Changes in the characteristics of disturbance regimes can, therefore, profoundly alter the composition and successional trajectory of a community and development of the ecosystem. It is important to note that disturbances that are facilitated by invasions, or disturbances that facilitate invasions (see driver-passenger concept following), are (1) not always discrete events in time (e.g., feral animal grazing or alterations in river hydrology); (2) may be chemical in nature (e.g., changes in nutrient cycling), not merely physical or structural; and (3) may not only increase but also reduce resource or substrate availability (e.g., reducing vegetative turnover or water availability).

Disturbances, or changes in disturbance regimes, are widely assumed to promote biological invasions. First, the invasibility of communities can be increased by disrupting species interactions, opening up sites for occupation (Sher and Hyatt 1999). Moreover, if the disturbance includes directional changes (e.g., a shift in abiotic conditions), the environment can become increasingly less hospitable for native species. In this sense, invasives can be regarded as passengers of disturbance (MacDougall and Turkington 2005). Riparian ecosystems, for example, are particularly prone to plant invasions, with invaders exploiting opportunities created by natural flood events and by anthropogenic disturbances (Richardson et al. 2007). Disturbances can also decrease the probability of invasion success, and natural disturbances have been shown to prevent or slow invasions (Buckley et al. 2007). The reintroduction of natural disturbances, such as flood regimes, has been suggested as a way to control or mitigate invasions.

Invasives can also be regarded as drivers of disturbance (MacDougall and Turkington 2005). Invasives can either cause changes in disturbance regimes or even introduce disturbance regimes that are novel to the system (Fig. 16.1). Invasive grass species, for example, are well known for changing fire regimes, altering fire severity and frequencies, or invading formerly fire-free environments (D'Antonio and Vitousek 1992). These alterations can lead to a positive feedback for the invader, with more invader biomass leading to higher fuel loads and hence increased fire

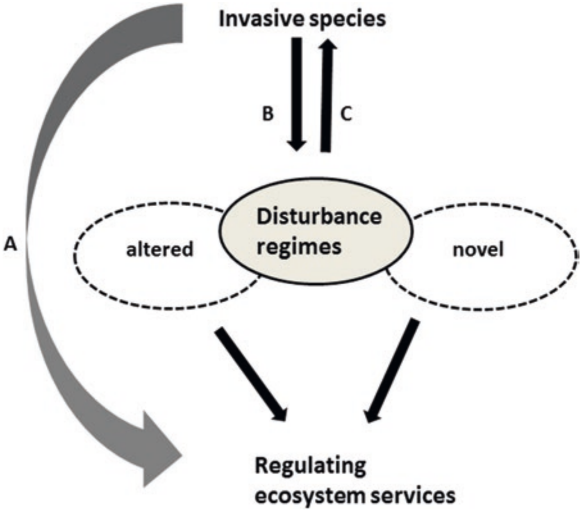

Fig. 16.1 Invasive species can impact on ecosystem services directly (A) or indirectly by altering disturbance regimes (B). Alteration in disturbance regimes can either be a change of an existing disturbance regime (altered) or the introduction of a disturbance regime that is novel to a given system. At the same time disturbances can impact on invasions (C), either increasing the probability of invasion success or preventing or slowing invasions. Table 16.1 summarises examples of different types of impacts on disturbance regimes

frequency and severity. This, in turn, results in greater invasive species recruitment and more biomass coupled with a reduction of native species recruitment (Rossiter et al. 2003). Introduction of invasive grasses in 'fire-free' systems can lead to the establishment of 'novel' fire regimes leading to dramatic changes in plant species composition and structure (D'Antonio et al. 2011).

The aim of this chapter is to review the evidence of the relationship between animal and plant invasions and changes in disturbance regimes and their synergies. We also explore the consequences that changes in disturbance regimes brought about by invasions can have on regulating ecosystem services.

16.2 Invaders as Drivers of Change in Disturbance Regimes

Invasive species have the potential to either introduce novel disturbance regimes or to alter existing disturbance regimes both in systems that were intact before invasion and in previously degraded systems. Changes in disturbance regimes can be triggered if invaders act as biotic disturbance agents, if invaders interact with physical forces of disturbance, or by the introduction of novel functional traits. Following we provide examples for changes in disturbance regimes triggered by invasions and discuss the effects of these on native ecosystems (for an overview, see Table 16.1 and Fig. 16.2).

Table 16.1 Invasion can cause alterations in disturbance regimes by either changing existing disturbance regimes or by introducing novel disturbances

Taxa	Novel disturbance regime	Altered disturbance regime
Invasive animals: mammalian herbivores	The wild boar (*Sus scrofa*) invasions in Hawaiian island habitats that evolved in the absence of large mammalian herbivores introduce disturbances such as tilling and grubbing (Barrios-Garcia and Ballari 2012).	Invasive beaver *Castor canadensis* foraging can change flooding regimes in Tierra del Fuego, Argentina (Lizarralde 1993).
	Introduced mammalian herbivores such as Australian brushtail possums *Trichosurus vulpecula* and wild deer *Cervus elaphus* in New Zealand forests change vegetation structure and composition (Peltzer et al. 2010 and references therein).	
Detrivores	Invasive European earthworms *Lumbricidae* in New Zealand pastures significantly increase decomposition and plant production through soil mixing (Mack and D'Antonio 1998).	Invasive earthworms in temperate forests of North America alter soil structure through burrowing and casting (Bohlen et al. 2004).
Plant invasions	Grass invasion introducing fire into 'fire-free' Hawaiian woodlands (D'Antonio et al. 2011).	Grass invasion in Australia and woody invasion in South Africa can increase fuels and hence fire frequency and severity, replacing or displacing native vegetation (Rossiter et al. 2003; Le Maitre et al. 2011, 2014).
		Brazilian pepper tree *Schinus terebinthifolius* can reduce fire frequency and severity in an otherwise fire-dependent pine savanna ecosystem in southeastern USA, reinforcing the conversion of native savanna into an invasion dominated forest (Stevens and Beckage 2009).
		Tree invasions in riparian ecosystems can modify sediment dynamics and increase stream bank erosion changing flooding regimes (Tickner et al. 2001).

Fig. 16.2 Examples of invasions, either changing existing disturbance regimes or introducing novel disturbances. *Top left*: Increased fire frequency with Gamba grass invasion in Australian woodlands (Photograph by N.A. Rossiter-Rachor). *Top right*: Grubbing of wild boar in forested communities in Hawaii (Photograph by Pat Bily). *Bottom left*: Pine invasion in South African fynbos leading to increases in fire frequency and severity (Photograph by David le Maitre). *Bottom right*: Eucalyptus invasion in riparian ecosystem in the Western Cape, South Africa, modifying sediment dynamics and increasing stream bank erosion (Photograph by David le Maitre)

Invaders can act as biotic disturbance agents. For example, wild boar, feral goats, and sheep on islands are contributing to soil disturbance and loss (Mack and D'Antonio 1998 and references therein). The wild boar, *Sus scrofa*, is an invading animal that has introduced a novel disturbance regime (Mack and D'Antonio 1998) in Hawaiian island habitats that evolved in the absence of large mammalian herbivores. Studies in forested communities in Hawaii have shown that wild boar invasion leads to removal or replacement of the herbaceous understory, which may lead to alteration in the soil nutrient retention capacity. Removal of the herbaceous understory can also negatively affect native birds by reducing the abundance and amount of nectar produced by plants, such as the Hawaiian raspberry, *Rubus hawaiiensis* (Barrios-Garcia and Ballari 2012 and references therein).

Non-native insect invasions can lead to increases in the frequency and intensity of defoliation events. Well-studied examples are the Hemlock woolly adelgid, *Adelges tsugae*, and the gypsy moth, *Lymantria dispar* (Ehrenfeld 2010 and references therein). Another functional group that has been found to alter disturbance regimes are detritivores. Invasive European earthworms of the Lumbricidae family in New Zealand pastures have been reported to significantly increase decomposition and plant production through soil mixing, whereas European earthworm invasions in northern temperate forests in the USA lead to changes in soil nutrient cycling (Mack and D'Antonio 1998; Bohlen et al. 2004).

Invaders can interact with physical forces of disturbance by, for example, increasing or decreasing fire frequency and intensity (Brooks et al. 2004), or by affecting geomorphological processes that either increase or decrease erosion rates on riverbanks. Invasion by the black wattle, *Acacia mearnsii*, in South African riparian ecosystems modifies sediment dynamics and can increase stream bank erosion (Rowntree 1991). Similarly, changes in flooding regimes have been ascribed to saltcedar (*Tamarix* spp.) invasions (Tickner et al. 2001) and to foraging/activities of the invasive North American beaver, *Castor canadensis* (Lizarralde 1993).

Invasive plants can also bring in new traits in the introduced community that interact with biological disturbance of grazing or fire regimes (Mack and D'Antonio 1998). For example, te Beest et al. (2015) showed that Siam weed, *Chromolaena odorata*, in South African mesic savannas has higher specific leaf area and leaf area index than native species, which enables this species to grow faster and produce more biomass, resulting in higher nutrient levels. This advantage enables the plant to intercept more light and reduce available moisture, thereby impacting native vegetation, ecosystem processes, and fire regimes.

16.3 Synergies Between Invaders and Altered Disturbance Regimes

Changes in disturbance regimes can result in an establishment of reinforcing feedback loops between the disturbance and the invader, thereby promoting the invader to the disadvantage of the native species (Mack and D'Antonio 1998). Changes in feedback loops that promote the invader, to the detriment of the native species, can eventually lead to regime shifts (i.e., altered states of ecosystem structure and function that are difficult or impossible to reverse) (Gaertner et al. 2014). *Acacia* invasion in South African fynbos, for example, triggers substantial changes in the soil nutrient cycling and the natural fire regimes, through the establishment of reinforcing feedback loops, which eventually results in a change from natural shrubland vegetation to dense *Acacia* woodlands with depleted native seed banks (Le Maitre et al. 2011). Dense *Acacia* invasions in riparian ecosystems typically suppress native vegetation cover and recovery rates, resulting in increased rates of sediment loss. Similarly, grass and forb invasions in California chaparral can establish reinforcing feedback loops through changes in the natural fire regimes, with long-term, infrequent fire events changing to short-term, frequent fire events. These changes lead to increases in non-native species cover and decreases in native species cover and diversity. Similar results have been reported for grass invasions in Australian savannas (Rossiter et al. 2003).

Feral horses, *Equus caballus*, and donkeys, *Equus asinus* released in western United States have established wild populations that graze heavily on native vegetation, promoting invasive non-native annuals that displace native perennials. Donkeys inhabiting the northwestern USA diminish the primary food sources of the native bighorn sheep, *Ovis canadensis*, and seed-eating birds, thereby reducing the abundance of these native animals (Pimentel et al. 2005). In Pennsylvania forests, overabundance of the invasive white-tailed deer, *Odocoileus virginianus*, has been shown to facilitate invasions by herbaceous plant species that tend to replace native species by modifying disturbance intensity and duration (Knight et al. 2009).

16.4 Impacts of Changes in Disturbance Regimes Caused by Invasions on Regulating Services

Although impacts of invasive species on provisioning ecosystem services are comparatively well quantified, the effects of invasions on regulating services are still relatively poorly understood, especially the link between changes in disturbance regimes triggered by invaders and changes in regulating ecosystem services, which has so far received little attention. Climate regulation and water flow regulation are two regulating services that can be highly altered by changes in disturbance regimes.

16.4.1 Climate Regulation by Altering Carbon Storage and Levels of Atmospheric Carbon Dioxide

Although carbon (C) fluxes (e.g., sequestration) rather than stocks link more directly to the ecosystem service of climate regulation, it has been suggested that C stocks can be altered by a range of different invasive species (e.g., plants, earthworms, and deer). Changes in C stocks are often related to changes in disturbance regimes caused by the invader. Also, the effects of invasive species can occur over short time scales (weeks to years), by directly affecting rates of primary production or decomposition, and over long time scales (decades and beyond), by causing compositional changes in the dominant native species (Peltzer et al. 2010).

Invasive mammals, insect herbivores, and plant pathogens can directly, and over a relatively short timeframe, affect carbon sequestration by increasing canopy disturbance through tree felling (e.g., beavers reintroduced to Finland and invasive in Chile) and defoliation [e.g., Australian brushtail possums, *Trichosurus vulpecula*, and invasive wild deer, *Cervus elaphus*, in New Zealand]. Increasing canopy disturbance, coupled with a disrupted subsequent recovery in terms of growth and recruitment of tree species, can have profound effects on C sequestration (Peltzer et al. 2010).

A well-known example of an indirect long-term effect on C sequestration is the increased fire intensity associated with grass invasion in forest ecosystems. Increased fire intensity alters tree population size structures towards increasing dominance by intermediate-size trees, reducing current live-tree C stocks and the potential for future C sequestration. Changes in fire regimes as a result of non-native grass invasions in woody ecosystems occur globally, throughout the western United States, Hawai'i, Brazil, and Australia (Peltzer et al. 2010). For example, invasive annual grasses, such as the cheat grass, *Bromus tectorum*, have replaced native sagebrush ecosystems in western North America by changing fire regimes. Transitions to a cheat grass post-fire community can result in a decrease in the ecosystem carbon storage capacity (Prater et al. 2006). Similarly, invasion by gamba grass, *Andropogon gayanus*, into the tropical savannas of northern Australia increases fuel loads, leading to changes in fire intensity and resulting in mortality of large trees combined with declines in live tree carbon (Rossiter et al. 2003), thus decreasing the potential for further C sequestration. In contrast, tree invasions into former treeless areas can lead to increases in ecosystem C stocks (Liao et al. 2008). Some fire-sensitive invasive species can introduce a fire-suppression feedback, reducing the frequency of fires to their own advantage. For example, the Brazilian pepper tree, *Schinus terebinthifolius*, can initiate a fire-suppression feedback in an otherwise fire-dependent pine savanna ecosystem in the southeastern USA, reinforcing the conversion of native savanna into an invasion-dominated forest (Stevens and Beckage 2009).

Another example for long-term effects on C sequestration through alterations in disturbance regimes are changes caused by invasive decomposers and detritivores. These invasive functional groups can alter forest soil C directly through decomposition or litter consumption and indirectly via altered biogeochemical processes and complex interactions across trophic levels (Peltzer et al. 2010). Invasive earthworms, for example, have been implicated in changed disturbance regimes, such as altered substrate mixing. Invasive earthworms in temperate forests of North America alter soil structure through burrowing and casting, processing litter, and redistributing organic matter. These alterations in the soil structure can lead to changes in the soil microbial community, and in nutrient cycling, which eventually leads to altered long-term forest C balances through soil C loss (Bohlen et al. 2004). Furthermore, the regeneration of both understory and canopy plant species can be suppressed by earthworm removal of surface organic layers. In some situations this can lead to the promotion of small-seeded, early-successional, low-biomass plant species rather than large-seeded, late-successional, high-biomass species. Thus, earthworms can affect long-term forest C balance not only through soil C loss but also by promoting successional changes in some cases.

16.4.2 Water Flow Regulation Affected by Changes in Land Cover

The flow regulation function is defined as the ability of watersheds and catchments to capture and store water from rainstorms, reducing direct runoff and flood peaks as well as releasing water more slowly so that flows are sustained into or through the dry season (Catford 2017). Plant invasions in dryland and riparian ecosystems can affect natural flow regulation by changing community structure and function in ways that increase evaporation losses and by increasing fuel loads in catchments so that fire severity and damage to soils are increased. South African fynbos ecosystems, for example, are prone to invasion by non-native trees, notably European pines and Australian acacias. Fynbos requires fire to regenerate, has moderate biomass, and occurs mostly in areas with a potential to erode. Fast-growing invasive species lead to increases in biomass and therefore in fuel loads. The greater fuel load increases fire intensity and severity which, in turn, changes the hydrological responses of catchments by decreasing infiltration and increasing soil erosion (Le Maitre et al. 2014). Alterations of disturbance regimes by invasive beaver into riparian areas can also lead to major ecosystem changes, including increases in flood risk (Gutierrez 2017).

Invasions by non-native plants can also alter the partitioning in the hydrological cycle, increasing evaporation and thereby decreasing river flows and groundwater recharge (Le Maitre et al. 2015). This alteration can reduce the amounts of water available from water supply schemes for agriculture and other human uses, as well as for the flows required to sustain river and estuarine ecosystems downstream. Invasions in river systems can also reduce the dry season flows, especially in Mediterranean environments where high transpiration rates for riparian invaders during the dry season can result in substantial water losses or complete cessation of flow (Le Maitre et al. 2015).

16.5 Conclusions

Invasions can significantly alter disturbance regimes by acting as biotic disturbance agents, by interacting with physical forces of disturbance or by the introduction of novel functional traits. Alterations in disturbance regimes can promote the invader to the detriment of the native species, especially if alterations lead to changes in reinforcing feedback loops. Ecological impacts range from changes in native community composition and structure to replacements of native species and to changes in ecosystem properties such as changes in soil nutrient cycling. Of particular concern are the less explored knock-on effects to ecosystem regulating services, such as on carbon sequestration and on water flow regulation, as these underpin human well-being.

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Part IV
Impacts on Cultural Services and Human Well-Being

Chapter 17
The Rise of Non-native Vectors and Reservoirs of Human Diseases

Wolfgang Rabitsch, Franz Essl, and Stefan Schindler

Abstract Globalisation has led to unprecedented changes in the distribution and incidence of human diseases. Pathogens, animal vectors, and reservoir species have been unintentionally displaced across natural geographic boundaries, resulting in serious human suffering and enormous economic costs. Non-native diseases can also threaten ecosystems and put ecosystem services and human well-being at risk. Introduced species and environmental interactions have caused manifold new risks and challenges for public health. Mosquitoes and ticks are the most important non-native vectors of human diseases, although many different species can serve as non-native reservoir hosts. In addition to imports as contaminants with cargo, the pet trade is an important pathway of introduction for non-native vectors and reservoirs. Evidence suggests that global environmental change will further facilitate emerging outbreaks of non-native human diseases, some of which may be re-emerging old foes. The complex interrelationships between native and non-native hosts, vectors, and pathogens entail inherent uncertainties and make predictions about future outbreaks very challenging. Natural ecosystems provide a regulating service for human well-being, and the loss of biodiversity therefore represents a serious threat to human health. The linkages between humans, animals, and environmental health are becoming more apparent and call for collaborative efforts ('One Health') towards a more responsible ecosystem stewardship.

Keywords Arthropods • One World One Health • Public health • Reservoirs • Vector-borne diseases • Zoonoses

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17.1 Introduction

Although only a minority of non-native species are known to have venoms, poisons, or toxins of human significance (Nentwig et al. 2017), some can accommodate and transmit pathogens and parasites of native and non-native origin relevant to human health. With the rise of globalisation, the numbers of non-native pathogens found in regions where they were previously absent have increased around the world (Jones et al. 2008; Smith and Guégan 2010). Well-known and less well known emerging infectious diseases appear in new regions, challenge taxonomists, medical diagnostics, and treatments, and may lead to human morbidity and death. The relationships between the agents of mischief are naturally complex, often crossing boundaries between environments and hosts, but can become even more shuffled by spillover (when a pathogen captures a novel host as a result of high pathogen abundance) and spillback (when a non-native host is competent for a native pathogen). Reservoir hosts, vectors, and pathogens may interact in all possible native/non-native combinations (Fig. 17.1). In addition, global change (e.g., climate change, habitat modification, urbanisation) affects species, their interactions, and their impact on human health. The inherent uncertainties—a characteristic feature of biological invasions in general—are truly magnified for non-native vectors and reservoirs of human diseases.

In addition, non-native species can have indirect human health impacts. For example, they can reduce the supply (1) of provisioning services by destroying harvests or depleting freshwater resources; (2) of regulating services by depleting natural regulation through competition or predation of native species; or (3) of cultural services by triggering modifications to human behavior and fashions in selecting vacation destinations or precautionary medical treatments. These effects often impinge most strongly on less developed economies and, although poverty is likely to decrease the probability of unintentional introductions of non-native species

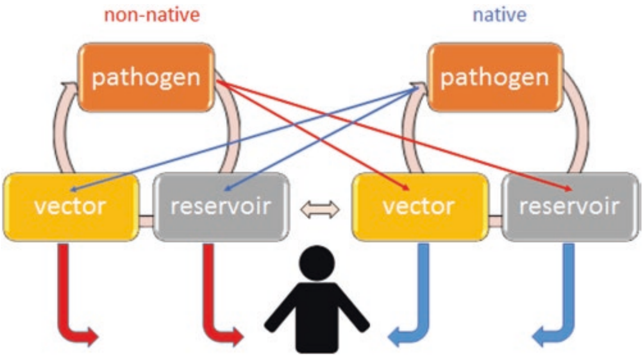

Fig. 17.1 Different kinds of interactions between native and non-native organisms can affect human health

Table 17.1 Definitions of key terms relevant for this chapter: other definitions may be applicable in other contexts

Term	Definition	Examples
Pathogen	The causative agent of disease: it may or may not be an organism.	Prions, virus, bacteria, fungi
Parasite	An organism living in or on another organism (its host) and obtaining its food from or at the expense of its host.	Protozoans, nematodes
Vector	An organism that carries and transmits pathogens from one organism to another.	Arthropods (e.g., mosquitoes, sandflies, ticks), mammals, birds, snails
Reservoir host	An organism that accommodates a pathogen, enables its survival and amplification, serves as source of infection for other host species, but does not take serious harm.	Mammals (most often rodents, bats, carnivores), birds, reptiles, snails
Definitive host	An organism that accommodates a pathogen, enables its reproduction, and suffers illness.	Humans (in case of human diseases)
Emerging (infectious) diseases	A disease with increasing appearance (incidence, impact, geographic or host range) in the past few decades.	Avian influenza H5N1, dengue fever, West Nile Fever
Zoonoses	Animal diseases that can be transmitted to humans.	Anthrax, influenza, lyme, rabies

because of lesser trade (Witt 2017), it also increases the probability of establishment, spread, and impact by the reduced availability of countermeasures.

The economic costs of non-native pathogens are also vast, including medical treatment and vector control, as well as indirect costs such as reduced availability for work and reduced on-the-job performance. The economic impact of the West Nile Virus disease in the United States between 1999 and 2013, for instance, was estimated as about US$780 million (Staples et al. 2014).

Here, brief accounts of selected non-native pathogens, vectors (with a particular focus on mosquitoes), and reservoirs are provided (Table 17.1). Pathogens and parasites that might be transmitted from pets to humans are also considered, but infections from livestock and animal products to humans (e.g., brucellosis, BSE) are excluded. The main drivers of introduction and spread are discussed, and examples are given in which the interaction with other non-native species indirectly facilitates health impacts by these diseases.

17.2 Non-native Pathogens and Parasites and Their Vectors

The most important non-native vectors of human diseases are arthropods, particularly mosquitoes, sandflies, fleas, lice, and ticks. Furthermore, there are around 100 arthropod-borne viruses (arboviruses) known that may give rise to human diseases. Most of the pathogens are introduced with reservoir hosts (including human travellers), with only a few presumably introduced with their vectors. However, after arrival in the new environment, the availability of suitable vectors is crucial to further spread.

There are many examples of pathogens of human diseases that have been recently translocated with their vectors or reservoir hosts beyond natural boundaries (Table 17.2). For instance, chikungunya virus (CHIKV), circulating in wildlife and domestic animal reservoir hosts, is transmitted by *Aedes* spp. mosquitoes (Fig. 17.2). It

Table 17.2 Selected human diseases, causative agents and their origin, vectors and recent outbreaks in non-native regions

Disease	Pathogen/ parasite	Origin	Vector(s)	Pathogen introduced with	Selected outbreaks in non-native regions
Chikungunya fever	Chikungunya virus	Africa-Asia (India)	*Aedes aegypti, A. albopictus*	Reservoir (human)	Italy (2007–2008), France (2010, 2014) Caribbean (2013), North and South America (2014)
Dengue Fever	Dengue virus	Tropical	*Aedes* spp.	Reservoir (human)	France, Croatia (2010), Madeira (2012)
Dirofilariasis	*Dirofilaria repens*	Southern Europe, Africa, Asia	*Aedes* spp. and other mosquitoes	Reservoir (animal), vector?	Belarus, Ukraine, Russia, Hungary, Poland, Austria, Czech Republic, Germany (2000s)
Leishmaniasis	*Leishmania* spp.	(sub) tropical, southern Europe	*Phlebotomus* spp., *Lutzomyia* spp.	Reservoir (animal)	Northern Italy, Germany (1990s)
Malaria	*Plasmodium* spp.	Africa, (southern Europe)	*Anopheles* spp.	Reservoir (human), Vector	Brazil, Colombia (2000s)
Plague	*Yersinia pestis*	China	Fleas (e.g., *Xenopsylla cheops*)	Reservoir (animal)	Madagascar (1990s)
Usutu fever	Usutu virus	Africa	Mosquitoes	Reservoir (animal)	Italy (2009)
West Nile fever, West Nile encephalitis	West Nile virus	Africa	*Culex* spp., *Aedes* spp., and other mosquitoes	Vector?	North America (1999)
Yellow fever	Yellow fever virus	Africa	*Aedes* spp. and other mosquitoes	Reservoir (human)	South America (since 1980s)
Zika fever	Zika virus	Africa-Asia	*Aedes* spp.	Reservoir (human)	Pacific (since 2007), Brazil (2015)

A representative selection of references can be found at www.cdc.gov

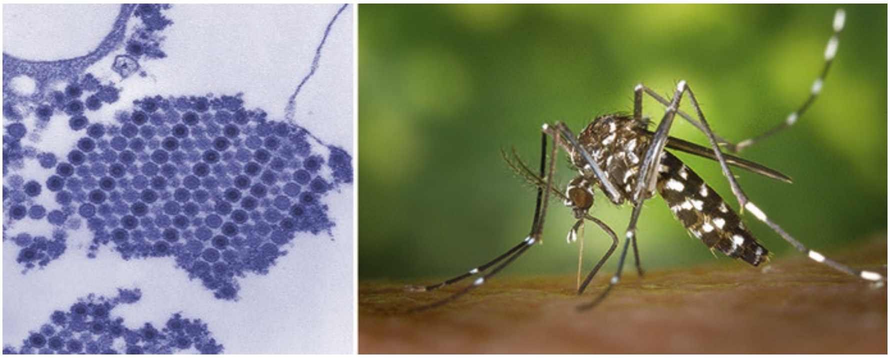

Fig. 17.2 Transmission electron micrograph of Chikungunya virus particles (Photograph by C. Goldsmith, CDC) (*left*) and adult female Asian tiger mosquito *Aedes albopictus* (Photograph by C. Goldsmith, CDC) (*right*)

was first detected outside its native tropical African-Asian origin in Italy in 2007, probably introduced by a traveller from India, causing a localised outbreak with some 200 cases. In 2010 and 2014, locally acquired infections were reported in southern France and in 2015 in Spain. During an epidemic outbreak on Reunion in 2005–2006, approximately one third of the human population became infected and 100 people died. It was demonstrated that the Reunion CHIKV-strain had higher infectivity for the introduced Asian tiger mosquito *Aedes albopictus* (compared to the native yellow fever mosquito *A. aegypti*) that led to more efficient transmission to hosts (Tsetsarkin et al. 2007). Such unpredictable changes in vector competence can facilitate the invasion of the pathogen and increase public health risks. In 2013, CHIKV was confirmed in the Western Hemisphere, in the Caribbean (Saint Martin), for the first time. In 2014, several cases were reported from people travelling from the Caribbean to Florida and Europe, and cases of a new African virus strain were confirmed in Brazil from army soldiers returning from Haiti. CHIKV is currently known in more than 40 countries in the Americas, with 176 human deaths and more than 1 million suspected cases (Fig. 17.3) attributed to this disease (www.who.int). The direct and indirect costs of the recent CHIKV outbreaks were estimated as more than US$50 million for Reunion (Soumahoro et al. 2011) and more than US$75 million for Jamaica.

Dengue virus (DENV) circulates in primates, including humans, and is also transmitted by *Aedes* spp. mosquitoes. The human health impacts can be asymptomatic (80 %), rarely severe, and very rarely life threatening (but more often in children) because of a hemorrhagic fever or dengue shock syndrome. It is suggested that the spread of the Old World tropical virus started in the sixteenth century with the slave trade from Africa. Infections have increased dramatically since the 1960s, with hundreds of millions of people infected yearly and probably four billion people at risk (Bhatt et al. 2013). Impoverished urban human settlements provide ample and uncontrolled breeding opportunities for the mosquito larvae. During the 1999 outbreak, a 20-fold increase of antibodies was found in blood samples from inhabitants in Mexico compared to adjoining inhabitants in Texas, which was traced

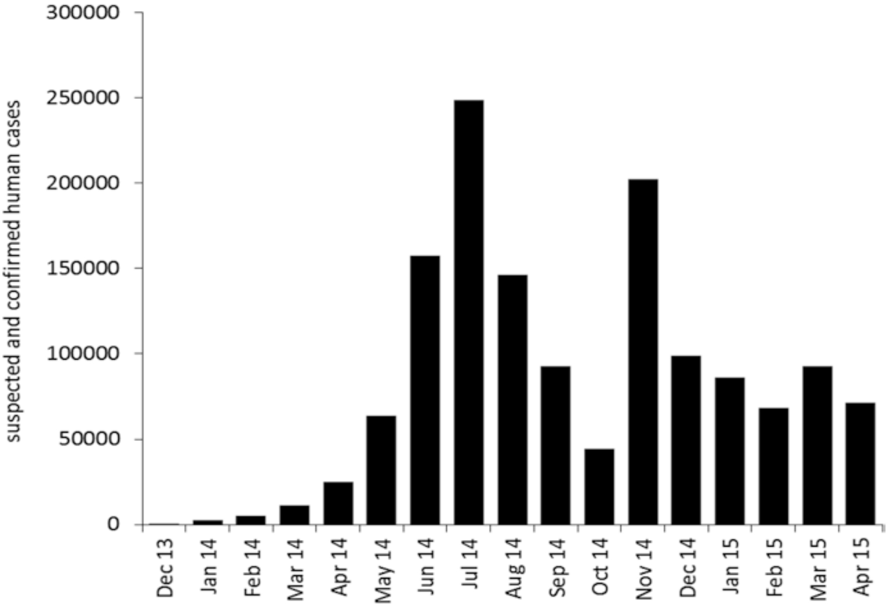

Fig. 17.3 Numbers of suspected and confirmed chikungunya cases by month in the Americas since its first record in December 2013 on Saint Martin (Data from www.cdc.gov)

back to the lack of air-conditioning in Texas (Reiter et al. 2003). DENV is regularly introduced to Europe by tourists from endemic tropical destinations, and it might rise again with the ongoing spread of the introduced vector *Aedes albopictus*. Local transmissions were reported from France and Croatia in 2010 and, in 2012, an outbreak on Madeira resulted in more than 2000 cases. Dengue infections have been estimated to cost US$1 billion per year in the Americas, excluding vector control.

Human dirofilariasis is caused by the nematode *Dirofilaria repens* and transmitted by mosquito species. Dogs are the most important reservoir hosts, but other carnivores are also suitable. It occurs in warmer climates in the Old World and is considered an emerging disease in temperate Europe, with increasing numbers of autochthonous cases. It is suggested that climate change, transport of dogs, and non-native mosquitoes have facilitated the spread into previously disease-free regions (Muro et al. 1999).

Leishmaniasis is a disease caused by different protozoan *Leishmania* species and transmitted by sandflies of the genera *Phlebotomus* and *Lutzomyia*. Dogs are the most important reservoir hosts, but it also circulates in wildlife (e.g., rodents). Different forms of the disease (visceral, cutaneous, mucocutaneous) are found in subtropical and tropical regions and in southern Europe, with some 12 million people infected globally. Genetic data suggest that *Leishmania infantum* was introduced from Europe to the New World some 500 years ago, most likely by conquistadores' dogs (Leblois et al. 2011). During the past decades, the parasites are increasingly imported directly with tourists or with infected dogs. Sporadic cases of locally acquired leishmaniasis and the increase in abundance and range of the vectors in Europe and North America, probably a result of climate change, suggest increasing relevance for public health (Dujardin et al. 2008).

Malaria is a tropical and subtropical disease of the Old World caused in humans typically by five protozoan *Plasmodium* spp. and transmitted by *Anopheles* spp. mosquitoes. There are approximately 200 million cases of malaria, with some 600,000 deaths in 2013, with the majority (90 %) occurring in Africa and striking children under 5 years (78 %) of age (www.who.int). However, thanks to progress in vector control and preventive therapies, since 2000 there has been a decline in infection prevalence and mortality rates worldwide. The historical distribution range also included temperate regions in Europe but, as a result of habitat modifications (drainage of wetlands) and chemical control, the disease largely disappeared in the 1970s. It resurfaced in the 1990s, particularly in Southeastern and Eastern Europe, and was pushed back again, but there is the permanent possibility of reintroduction and circulation as demonstrated by several cases in Greece between 2010 and 2013 (www.who.int). Malaria was introduced from Africa to the New World at the end of the fifteenth or in the sixteenth century. It might have arrived first on Cuba and soon spread to new suitable areas. An outbreak in Brazil in the 1930s was attributed to the introduction of the competent vector *Anopheles arabiensis* from Africa (Parmakelis et al. 2008). Nowadays, each year, several tens of thousands of infected international travellers directly introduce the parasite into their homelands (Gratz 2006). The so-called ‘airport-malaria’ describes rare cases of non-travelling people living near transportation hubs being bitten and infected by unintentionally introduced *Anopheles* vectors, and even rarer cases of ‘baggage-malaria’ have been suggested (Gallien et al. 2013).

Plague is a disease caused by the bacterium *Yersinia pestis*, transmitted (among others) by the Oriental rat flea, *Xenopsylla cheopis*, and by circulating in small vertebrates, most often rodents such as rats and squirrels. It can also be transmitted by contact, inhalation, or ingestion. Mortality in humans is high (up to 60 %) if untreated. It originates from China (Haensch et al. 2010) and has a long history including the Black Death pandemic in fourteenth-century Europe. Although globally decreasing in relevance, some 800 cases and 126 deaths were still reported in 2013 (www.who.int), most of which occurred in Africa, particularly on Madagascar, with increasing numbers of cases. Recent outbreaks might have been facilitated by habitat change and introduced rats. It was introduced to North America in 1900 by rats on ships, from whence it established a sylvatic cycle in native rodents. Currently, it is distributed in the western part of the United States, with approximately 1000 probable or confirmed cases since its introduction (www.cdc.gov).

Usutu virus (USUV) was first found outside its native African range in 2001, after a mass mortality of the common blackbird, *Turdus merula*, in Austria. It is assumed that the virus arrived along with migrating birds, but human translocation with infected pet birds cannot be entirely ruled out. It circulates in avian reservoir hosts and is only rarely transmitted to humans by the mosquito *Culex pipiens* complex. Although it is not considered a major public health concern, human infections were reported from Italy (Pecorari et al. 2009). Usutu fever causes fever and headaches and might have a fatal course in elderly and immunocompromised people. USUV is currently spreading in Europe, and incidences in birds are increasing (Vázquez et al. 2011).

West Nile virus (WNV) circulates in bird reservoir hosts and is transmitted to humans by *Culex* spp. and *Aedes* spp. mosquitoes. Its origin is believed to be in Africa, from whence it has spread to West Asia and Southern and Central Europe since the 1950s (Gratz 2006). It was inadvertently introduced to North America in 1999, presumably by an infected bird or mosquito on an airplane, and spread across the continent within a few years through various bird reservoirs with occasional spillover to humans; it is now widely established from Canada to Venezuela (Kilpatrick 2011). The spread was facilitated by the almost simultaneous arrival of the non-native Asian tiger mosquito in 1998. The virus causes 'West Nile fever' (20 % of the cases) and in rare cases 'West Nile encephalitis,' a life-threatening disease with elderly and immunocompromised people at greatest risk. Between 1999 and 2013, 1668 cases of death were documented in the USA (www.cdc.gov). One outbreak of WNV in California included 163 infected people at a cost of US$2 million for medical treatment and US$700,000 for mosquito control. One outbreak in Louisiana in 2003 infected 329 people, with costs estimated at more than US$20 million. It is expected that WNV will further spread and cause increasing public health impacts.

It is assumed that yellow fever virus was introduced at least twice to the New World on ships with the slave trade from Africa in the seventeenth and nineteenth centuries, causing thousands of deaths until development of a vaccine that ended the disease in 1905 in North America. It circulates in humans and other primates and is transmitted primarily by *Aedes aegypti* and other mosquito species. Cases have been increasing again in South America since the 1980s, probably because of reinvasion of urban areas by non-native *Aedes* spp., which benefit from limitations in vector control, vaccination programs, and eventually from climate change. It is assumed that in the event of re-emergence of the disease in tropical America, introduction into Asia and the Pacific is very likely.

The African-Asian Zika fever virus was introduced to the Pacific and recently to South America with infected travellers. Native and non-native *Aedes* spp. mosquitoes serve as vectors of the disease in its new range (Roth et al. 2014).

17.3 Non-native Reservoir Hosts

In this section, selected examples of non-native animal species that may serve as reservoir hosts for native or non-native pathogens of human diseases are presented. Transmission to humans may occur directly or via native or non-native vectors, most often arthropods.

Rodents are known as hosts of more than 60 zoonoses (Meerburg et al. 2009). Rats, *Rattus* spp., originated in Asia have expanded their geographic ranges as stowaways on ships together with human expansion and are known to host a large diver-

Fig. 17.4 Introduced semi-domesticated and pet rodents and birds (left: grey squirrel, *Sciurus carolinenis*, and right: Canada goose, *Branta canadensis*) may host and transmit native and non-native pathogens to humans. Their presence in urban habitats increases the likelihood of transmission. (Photograph by Wolfgang Rabitsch)

sity of pathogens: plague, salmonella, leptospirosis, tapeworms, murine typhus, tularaemia, and many others, including apparently undescribed strains. Firth et al. (2014) investigated the brown rat, *Rattus norvegicus*, in New York and found 15 bacterial and protozoan pathogens and, for the first time in the USA, Seoul hantavirus, which probably was only recently introduced. In Europe, introduced grey squirrels, *Sciurus carolinenis*, (Fig. 17.4) and Siberian chipmunks, *Eutamias sibiricus*, were found to be competent hosts of *Borrelia burgdorferi*, the agent of Lyme disease, increasing health risks by contributing to a higher density of infected vectors, that is, the native castor bean tick *Ixodes ricinus*.

Introduced raccoon dogs, *Nyctereutes procyonoides*, from East Asia and raccoons, *Procyon lotor*, from North America are suitable reservoirs and vectors of rabies. Western European countries have been declared free of rabies for decades, but this may change with spreading populations of both aforementioned non-native mammal species, which add to the native reservoir fauna and increase the likelihood of encounters with humans, specifically when invading urban habitats. The nematodes *Baylisascaris procyonis* and *Strongyloides procyonis* that were introduced with raccoons to Europe and Japan, respectively, rarely cause human cases of baylisascariasis, affecting brain tissue (Sorvillo et al. 2002), or strongyloidiasis, affecting the intestine (Sato et al. 2006).

In Japan, the small Indian mongoose, *Herpestes auropunctatus*, introduced to control snakes, carries antimicrobial-resistant strains of the bacterium *Escherichia coli* (Nakamura et al. 2011).

Non-native birds can harbor many pathogens of human concern. The Canada goose, *Branta canadensis*, (Fig. 17.4) deposits *Campylobacter*, *Enterococcus*, *Escherichia coli*, *Legionella*, *Girardia*, and *Cryptosporidium* with excreted droplets to lakes and urban greens. Parrots, pigeons, ducks, and other birds host the bacterium *Chlamydia psittaci*, which can cause psittacosis (ornithosis), a disease causing pneumonia in humans, but rarely (<1 %) leading to death. Bird owners and pet shop employees are at increased risk.

Finally, non-native pet reptiles such as the pond slider, *Trachemys scripta*, may carry *Salmonella* bacteria, which are usually transmitted via contact or smear infection, and ectoparasitic ticks that, albeit only rarely, can harbor human pathogens.

17.4 Drivers of Introduction and Spread

Global trade and international travel are the most important driving factors of the increasing incidence and emergence of non-native human diseases, both showing no signs of decline (Jones et al. 2008). Based on recent inventories, Schindler et al. (2015) listed more than 50 zoonotic non-native parasites, vectors, and hosts introduced to Europe. The Asian tiger mosquito was introduced in cargo containers with ornamental plants (e.g., lucky bamboo or bonsais) or used tires, where females deposit their eggs. However, living mosquitoes are also regularly introduced by airplanes (Scholte et al. 2014).

Another important pathway for non-native pathogens is the animal pet trade. Approximately 200 million animals are legally imported into the USA each year in the pet trade. Although pet animals are usually kept in enclosures (aquaria, terraria, aviaries), some might also be kept in 'semi-permeable' garden pools, free-range facilities, or zoos. Pre-border pathogen screening and risk analysis of wildlife species in the pet trade are considered essential to improve health protection (Smith et al. 2009). The 2003 outbreak of monkeypox in the USA was traced back to 762 African rodents imported for the pet trade from Ghana (www.cdc.gov). Between 2011 and 2013, three pet owners of the variegated squirrel, *Sciurus variegatoides*, which is native to Central America, died in Germany of encephalitis of a still unidentified bornavirus.

There is evidence that climate change affects native and non-native distribution ranges of hosts, vectors, and pathogens, provoking new species and environment interactions and facilitating 'novel' communities. Medlock and Leach (2015), for example, summarised the possible effects of climate change on vectors and vector-borne diseases in the UK and suggested that southeast England will become more suitable for the establishment of the Asian tiger mosquito and non-native ticks. Several models suggest global rearrangements of distribution areas for mosquito species (Campbell et al. 2015), with large uncertainties from the lack of high-resolution distribution data. Climate change may also free previously infested areas from health threats if areas become unsuitable for survival of the causative agents.

Moreover, landscape urbanisation appears to also be a key for many emerging vector-borne human diseases. Increasing exposure to diseases as the result of closer contacts between humans and reservoirs, vectors, and pathogens often results from underdeveloped dwellings in suburban settlements with low control possibilities. Habitat fragmentation, destruction, and deterioration also contribute to the rise of some pathogens. For example, deforestation in tropical areas has increased the risk of malaria and other diseases by creating a more suitable habitat for vector species. Natural ecosystems, therefore, provide a regulating service for human well-being, and loss of biodiversity represents a serious threat to human health (Keesing et al. 2010).

Non-native species might indirectly facilitate health impacts by interacting with non-native pathogens, vectors, and reservoirs. For example, feral pigs have facilitated the spread of avian malaria in Hawai'i by creating breeding habitats for mosquitoes in forests, and invasion of the wild sage, *Lantana camara*, has provided novel habitats for the native tsetse flies, *Glossina* spp., which are vectors of human sleeping sickness in Africa. In the eastern USA, the ornamental Japanese barberry, *Berberis thunbergii*, provides foraging sites for ticks carrying *Borrelia burgdorferi*, the causal agent of Lyme disease. Similarly, in South America, fruit availability of non-native bamboos seems to support rodent populations carrying hantaviruses that cause hemorrhagic fever in humans.

Non-native parasites might also change the ecological host–parasite interactions and networks via, for example, dilution effects (less competent non-native hosts reduce disease prevalence in populations of more competent native hosts), sink effects (the non-native host pulls off parasites from native hosts), or amplification effects (non-native hosts increase the risk of transmission), with substantial consequences for wildlife and human health (Hatcher and Dunn 2011).

Finally, it has to be mentioned that pathogens have been introduced intentionally into laboratories to be tested for biological warfare. The African Marburg virus was noticed during outbreaks in Germany and former Yugoslavia in 1967 when laboratory workers became accidentally infected, and in 2006, media reported mice infected with plague had escaped from an anti-bioterrorism research facility in New Jersey.

17.5 Conclusions

The patterns and processes of emerging infectious diseases, parasites, and biological invasions share similarities, and there is a great opportunity for cross-fertilisation of theoretical concepts and practical management actions (Hatcher and Dunn 2011). There is a need for multidisciplinary research efforts to directly link the spread and abundance of non-native vector and reservoir species to environmental changes and to changes in the severity of human health impacts (Rabinowitz and Conti 2013; Schindler et al. 2015). The 'One World One Health' initiative seeks to build a bridge between human and veterinary medicine disciplines and sectors to promote better understanding and unite collaborative efforts for better health outcomes for people, animals, and the environment (www.onehealthinitiative.com). Specifically, it advocates for a better understanding of the introduction, spread, and control of non-native diseases and vectors, as well as joint efforts in education and outreach to the public and decision makers. The Convention on Biological Diversity (CBD) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) should reinforce their participation to this strategic framework, developed by the FAO, WHO, and OIE.

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Chapter 18
Impact of Non-native Animals and Plants on Human Health

Wolfgang Nentwig, Dietrich Mebs, and Montserrat Vilà

Abstract Although many non-native species have human health impacts, especially as vectors of diseases, a minority are known to have venoms, poisons, and toxins of human significance, or to cause allergic reactions. Among animals, these effects are known in only a few taxonomic groups, where marine species are particularly well represented (e.g., jellyfish, mollusks, fish). A few venomous or toxic fish species cause acute burning pain, whereas systemic health symptoms are rare. Terrestrial animals that are famous for venomous bites and stings, such as scorpions and snakes, are relatively underrepresented as non-native species causing health problems. Insects such as bees, wasps, and ants are the most important group insofar as human health is concerned. Impacts usually include bites, stings, and certain injuries, but with jellyfish, skin contact alone is sufficient to produce severe dermatitis. In the case of animals possessing venom glands, a wide array of toxic compounds is injected, often with serious and even lethal consequences. A particularly dangerous situation results from mass attacks of bees, wasps, or ants in which multiple stings may be received. This behaviour is common in Africanized honeybees and accounts for their being the non-native species that has caused most human fatalities. Some non-native plant parts, especially fruits, are toxic if ingested. The sap of several plants can also be an irritant and cause dermatitis by contact, and in other cases spines and thorns can cause skin rashes. The major human health hazard posed by non-native plants is their allergenic pollen. The copious allergenic airborne pollen produced by some non-native ornamental tree plantings, even in areas where establishment has not occurred, highlights the fact that risks to human health for some non-native plant species do not require invasion.

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18.1 Introduction

Human health implications of non-native species has largely focused on species known to carry and transmit pathogens or parasites, especially mites and dipterans (Rabitsch et al. 2017), but much less information is available regarding other direct health impacts. A broad spectrum of non-native species present non-vectored health issues for humans, covering several higher taxa, but there are often only a few species within a group of concern. For example, most snakes and scorpions are underrepresented as non-native species. Health issues caused by non-native species may be very diverse because these species may contain or accumulate a diverse array of noxious substances including poisons and toxins; they may also sting or bite humans, causing envenoming, injuries, allergic reactions, and secondary infections. All these aspects may lead to lethal outcomes and may drastically increase health costs.

Venoms, poisons, and toxins are substances that impact biological functions in other organisms. Venomous organisms differ from poisonous organisms in that they inject venom from storage cells or glands into other organisms, whereas the poisons are contained in some organs (skin, leaves), or in the whole body, so that other organisms are affected by touching or eating them. This review discusses the four non-vectored main health impacts (i.e., venoms, poisons, allergies, and injuries) caused by non-native animal and plant species in terrestrial, freshwater, and marine ecosystems. Information is also given on the medical complications caused by the impacts of these species and as well as descriptions on their areas of origin and pathway of introduction.

18.2 Invasive Venomous Species

18.2.1 *Scyphozoa*

Scyphozoa are marine jellyfish species with a medusa as the dominant stage of their life cycle. They capture their prey or defend themselves against predators with nematocysts present in their tentacles and oral arms around the central mouth that sting upon contact. At least three scyphozoan species have spread to other oceans, usually in ballast water, and through infrastructure corridors such as Lessepsian migrants via the Suez Canal.

The nomadic jellyfish, *Rhopilema nomadica*, is indigenous to the tropical waters of the Indian and Pacific Oceans and has been spreading through the Suez Canal into the eastern Mediterranean Sea since the 1970s. It can cause painful dermatitis to humans by skin contact. Its presence in the Levantine coast causes a nuisance to summer tourists. The floating bell, *Phyllorhiza punctata*, is native to the West Pacific from Australia to Japan, but it has been widely introduced to Hawaii, the Gulf of Mexico, and the Mediterranean Sea with ballast water. It has a mild venom and is not considered a major threat to humans, but because of its major impact on fisheries, it is listed among the 100 worst invasive species of the world (GISD 2015). The upside-down jellyfish, *Cassiopea andromeda*, is common in tropical and subtropical shallow waters, such as in mangrove areas of the Atlantic, Pacific, and Indo-Pacific. It entered the Mediterranean Sea through the Suez Canal. Upon skin contact, the stings often provoke a mild reaction only, but more sensitive individuals may exhibit stronger symptoms, including pain, itchy rash, swelling, and vomiting.

18.2.2 Arthropoda

Araneae After insects, spiders constitute the most diverse terrestrial invertebrate group. However, few non-native spider species are able to establish in the regions where they are introduced. For example, in Europe there are only 50 non-native spider species compared to more than 1300 non-native insect species (Nentwig 2015). Most spider species possess a pair of venom glands in the prosoma; they inject venom into prey items or, in rare cases, use it as defence when threatened. Spider venom is a complex mixture of highly active neurotoxins and other compounds (Kuhn-Nentwig et al. 2011), which are usually not lethal to large vertebrates including humans (Nentwig and Kuhn-Nentwig 2013). Moreover, because of their small body size, most spiders are not capable of penetrating human skin with the fangs of their chelicerae. Spiders mainly spread as contaminants of traded commodities (potted plants, fruits) or as stowaways in transport containers.

Of some 35 venomous black widow spider species, *Latrodectus* spp., only a few have been introduced to other biogeographic regions of the world: both *L. geometricus* from South America and *L. mactans* from North America have spread to many other countries, and the Australian *L. hasselti* (Fig. 18.1) has spread to Asia and Japan. Bites to humans occur occasionally, but they pose only moderate health risks. In some cases of spider bite (latrodectism), acute envenoming symptoms, such as general pain persisting for 12–24 h after the bite, may require medical attention, but death is very rare and appears to be caused by secondary infections and other complications, not by direct venom effects (Nentwig and Kuhn-Nentwig 2013).

There are some 100 species of venomous brown or violin spiders, *Loxosceles* spp., with most of them from the Neotropics. Only a few have been introduced to other continents: *L. gaucho* from South America, which occurs in Tunisia; *L. laeta* from North America, which has spread to Finland and Australia; *L. rufescens*, probably from the Mediterranean, which now has a cosmopolitan distribution. Because of the secretive nature of *Loxosceles* spiders, bites are uncommon. *Loxosceles*

Fig. 18.1 The redback spider or Australian black widow, *Latrodectus hasselti*, has spread from Australia to New Zealand and to several Asian countries including Japan. Its bite poses moderate health risks and may require medical attention (Photograph by D. Mebs)

venom contains an enzyme (sphingomyelinase D) that causes severe local skin necrosis and a deep ulcerating wound (cutaneous loxoscelism) that heals slowly and can require skin grafting. Systemic reactions are rare and are characterised by severe intravascular haemolysis and disseminated intravascular coagulation, eventually leading to renal failure and death, particularly in children (Da Silva et al. 2004; Vetter 2015).

The woodlouse spider, *Dysdera crocata*, native to the Mediterranean area, has been introduced to most other continents and now has a cosmopolitan distribution. Because of the considerable size of the spider (10 mm body length), its unusual large and powerful chelicerae, and its synanthropic lifestyle, bites of humans occur occasionally. The venom causes minor pain, typically lasting for less than 1 h, followed by local erythema and swelling (Vetter and Isbister 2006).

The white-tailed spiders, *Lampona cylindrata* and *Lampona murina*, are native to Australia but have been introduced to New Zealand. They colonise houses and gardens, and bites frequently occur, especially because the spiders like to hide in clothing or towels. In most cases bites are local (pain and swelling), rarely systemic (nausea or headache), and symptoms are mild (Isbister and Gray 2003).

At the psychological level, irrespectively of the species origin, spiders may cause phobic reactions in people. Media reporting on the arrival of a new venomous spider may increase arachnophobia. It does not help to state that the perception of the problem is much bigger than the physical danger they might cause to people. Despite this, and the fact that arachnophobia is well known and probably present in all modern societies, there is as yet no research evaluating the impact of non-native spiders on arachnophobia.

Insecta The only non-native insects that cause significant non-vectored health problems to humans are hymenopterans from three families, the bees, wasps, and ants. In each family, the female workers have an ovipositor that is no longer used for egg laying but has been transformed to a stinging apparatus with a venom gland to defend themselves and/or their nest. Because the nests of some species may contain hundreds or thousands of individuals, when attacked humans may receive multiple stings.

Apidae Africanized honeybees *Apis mellifera scutellata* (also called "killer bees") have highly aggressive behaviour (Morales et al. 2017). They attack in large numbers and pursue their victim for more than 500 m. The venom consists of peptides and enzymes, such as phospholipase A_2 and hyaluronidase, but there is no major difference between the venom of Africanized and European honeybees. A large number of stings, such as 200–1000, is fatal, particularly in children. According to a rough estimate, more than 1000 people died in the first 35 years following the introduction of these bees to Brazil (Franca et al. 1994).

Vespidae The German wasp, *Vespula germanica*, is native to the Western Palearctic and has been introduced to the Americas, Australia, and New Zealand, whereas the common wasp, *V. vulgaris*, a Holarctic species, has been introduced to Australia and New Zealand. The common wasp is listed among the 100 worst invasive species of the world (GISD 2015). Queens of both species can easily be dispersed as stowaways with cargo. Although these wasps are considered not to be aggressive, they may sting when disturbed. The Asian black hornet, *Vespa velutina*, is native to Southeast Asia and has recently been introduced to South Korea, Japan, and Mediterranean Europe, probably with cargo. This species is not aggressive, but stings when people approach its nests. Multiple stings may occur because wasps release an alarm pheromone during the stinging process. Because venoms of wasps, hornets, or bees are highly potent allergens, humans may be sensitised by one sting only and, following the next sting, may experience an immediate severe general allergic reaction with life-threatening anaphylactic shock symptoms requiring urgent medical intervention. About 40 deaths per year have been estimated for the United States (Schmidt 1986). Stings also incur costs when people visit general practitioners or need hospitalisation, by causing deaths, or when wasp attacks result in car accidents. A recent study estimated such costs for New Zealand as NZ$1.1 million per year (MacIntyre and Hellstrom 2015).

Formicidae Four of the six ant species mentioned here are listed among the 100 worst invasive species of the world (GISD 2015), mainly because of their enormous environmental impact as generalist predators, but also because they sting people and cause significant economic damage. These ants were globally spread as stowaway with cargo and now have a nearly cosmopolitan distribution.

The imported red fire ant, *Solenopsis invicta*, and other *Solenopsis* species, mainly *S. geminata* and *S. richteri*, are native to South America and have been introduced to North America, China, Australia, and many Pacific islands. Fire ants are highly aggressive and they react rapidly to any disturbance. A fire ant can sting repeatedly, even after depletion of their venom gland. The sting causes an immediate strong, local burning ("fire") sensation, followed by erythema and swelling of the affected skin area. In some cases, the sting may cause severe allergic reactions, and even fatal anaphylactic shock has been reported (Steigelman and Freeman 2013). The little fire ant, *Wasmania auropunctata*, is native to Central and South America, but can now be found in many parts of the world, excluding Asia. It is abundant in agricultural areas and stings people working in the field. The crazy ant, *Anoplolepis gracilipes* (= *A. longipes*), probably originated from Africa and has been introduced to South America, Asia, and Australia, and the Argentine ant, *Linepithema humile*, native to Argentina, now occurs throughout the world. Both species defend themselves by applying painful and irritant stings.

18.2.3 Fish

Scorpionfishes are a species-rich family mainly of tropical seas. One quarter of the species possess venom glands in the numerous spines in their fins. A sting causes immediate strong local pain and oedema, but generalised symptoms (nausea, syncope, muscle weakness) are rare (Kizer et al. 1971), and no fatalities have been reported. The lionfish *Pterois volitans* (Fig. 18.2) is a Pacific species that invaded the Atlantic coast of the USA and the Caribbean Sea via ballast water or was released as a pet by aquarium keepers. The Indo-Pacific *P. miles* reached the Eastern Mediterranean via the Suez Canal. Rabbitfishes are a small family of coral reef fishes in the Indo-Pacific. They also possess numerous spines with venom glands. A sting provokes immediate but not long-lasting pain. Two species, the marbled spinefoot *Siganus rivulatus*, and the dusky spinefoot *S. luridus*, entered the Mediterranean Sea through the Suez Canal. Mainly fishermen are stung by the fish when emptying their nets. Eeltail catfish are another small family of fish species in the Indo-Pacific or adjacent freshwaters. The first spines of their dorsal fin and of both pectoral fins are large and serrated, with venom glands attached. A sting causes pain, oedema, and bleeding wounds. Systemic symptoms, such as nausea and hypotension, are rare. The only non-native species of this group, the striped eel catfish *Plotosus lineatus*, also entered the Eastern Mediterranean via the Suez Canal.

Fig. 18.2 The lionfish, *Pterois volitans*, was transferred with ballast water from the Pacific to the Caribbean Sea and the Atlantic coast of the USA, or was released by pet owners. Its sting causes immediate strong local pain (Photograph by W. Werzmirzowsky)

18.2.4 Snakes

The brown tree snake, *Boiga irregularis*, native to Southeast Asia, was deliberately introduced to Guam to keep rats and mice under control. Because of the lack of natural predators, the snake proliferated tremendously and became a pest, causing the decline and almost extirpation of indigenous birds, bats, and lizards on the island. This rear-fanged colubrid snake is only mildly venomous, but it reacts aggressively when encountered. Numerous bites occur in Guam, producing painful local reactions, swelling, and blistering. More serious symptoms have been reported, particularly in children, including muscular weakness, ptosis, and even respiratory arrest (Fritts et al. 1994). Mackessy et al. (2006) identified a number of peptides as suspected neurotoxins in the venom, which may explain the paralytic symptoms observed in human envenoming. The snake is listed among the 100 worst invasive species of the world (GISD 2015).

18.3 Invasive Poisonous Species

18.3.1 Fish

Poisonous fish also entered and colonised the eastern Mediterranean Sea via the Suez Canal. The pufferfish, *Lagocephalus sceleratus*, native to the Indian and Pacific Oceans, contains tetrodotoxin in its skin and organs. Tetrodotoxin is a powerful toxin that specifically blocks voltage-gated sodium channels and inhibits nerve transmission. When the fish is consumed, severe poisoning symptoms occur that are often lethal as the result of respiratory paralysis. Over recent years, populations have tremendously increased along the coast of Israel and southern Turkey. As local fishermen seem to be unaware of the danger, they catch the fish, which eventually appear in local markets, becoming a public health issue. Local emergency organisations have been alerted regarding the potential risks of consuming pufferfish (Bentur et al. 2008; Beköz et al. 2013).

18.3.2 Plants

Some non-native plants have secondary metabolites that are toxic to humans if ingested (Table 18.1). The oleander shrub, *Nerium oleander*, is native to riverine habitats of South Spain and Northern Africa. The beautiful flowers and high tolerance to summer drought of *N. oleander* have promoted its extensive use in gardening and restoration in other Mediterranean regions, such as in California. All plant parts contain cardiac glycosides that if ingested affect the heart, the gastrointestinal system, and the central nervous system. In the USA several hundreds of cases of poisoning per year have been reported (Watson et al. 2003), of which 3 cases have been fatal. Foxglove, *Digitalis purpurea*, native from temperate Europe and introduced in other parts of the world as an ornamental, also contains cardiac glycosides. Berries from some non-native species (e.g., Solanaceae) contain alkaloids that are toxic to vertebrates, including humans, if ingested. Symptoms of poisoning include salivation, respiratory complications, trembling, and diarrhoea. The berries of the European black nightshade, *Solanum nigrum*, are an important contaminant of peas that can lead to ill health upon ingestion and thus increase the costs of processing.

Dermatitis is one of the main health hazards caused by some non-native plants. The giant hogweed, *Heracleum mantegazzianum*, is a tall monocarpic herb that has been introduced in horticulture in central Europe and North America. Plant skin contact can cause phytophotodermatitis caused by the UV photo-activation of furanocoumarins present in the sap. The sap of the tree of heaven, *Ailanthus altissima*, is also toxic. It can cause eczema and, after long exposure, can produce myocarditis from the plant quassinoid proteins (Bisognano et al. 2005). Santa Maria feverfew, *Parthenium hysterophorus*, has been introduced in Asia with cereal grains imported from the USA and is spreading in agricultural and forested areas. In Nepal, fodder

Table 18.1 Selected non-native plant and animal species with human health impacts. Pathway terminology according to Hulme et al. (2008) (see text for details)

Species	Common name	Higher taxon	Area of origin	Invaded area	Pathway	Human health impact	Fatal issues in invaded area
Rhopilema nomadica	Nomad jellyfish	Jellyfish	Indian and Pacific Ocean	Mediterranean Sea	Corridor	Painful dermatitis	No
Latrodectus geometricus	Brown widow spider	Spider	South America	Cosmopolitan	Contaminant, stowaway	Bites	No
Apis mellifera	Africanized honeybee	Insect	Africa	South and North America	Escape	Numerous stings	Yes
Vespula germanica	German wasp	Insect	Europe	Americas, Australia	Stowaway	Numerous stings	Yes
Solenopsis invicta	Imported red fire ant	Insect	South America	North America, China, Australia	Stowaway	Numerous stings	Yes
Lymantria dispar dispar	European gypsy moth	Insect	Europe	North America	Contaminant	Dermatitis, allergic reaction	No
Aedes albopictus	Tiger mosquito	Insect	Southeast Asia	All other continents	Stowaway	Painful bites, vector of parasites	No
Ensis americanus	American jackknife clam	Mollusk	American Atlantic coast	European Atlantic coast	Stowaway	Injuries	No
Pterois volitans	Lion fish	Fish	Pacific	Atlantic	Stowaway, escape	Stings	No
Lagocephalus sceleratus	Pufferfish	Fish	Indian and Pacific Ocean	Mediterranean Sea	Corridor	Toxins	Yes
Boiga irregularis	Brown tree snake	Snake	Southeast Asia	Guam	Release	Bites	No
Ambrosia artemisiifolia	Ragweed	Plant	North America	All other continents	Contaminant	Allergic reaction	No

(continued)

Table 18.1 (continued)

Species	Common name	Higher taxon	Area of origin	Invaded area	Pathway	Human health impact	Fatal issues in invaded area
Ailanthus altissima	Tree of heaven	Plant	Southeast Asia	All other continents	Release	Toxins, dermatitis, vomiting	No
Eucalyptus spp.	Eucalyptus	Plant	Australia	All other continents	Release	Allergic reaction	No
Acacia spp.	Acacia	Plant	Australia	All other continents	Release	Allergic reaction	No
Xanthium spp.	Cocklebur	Plant	America	All other continents	Contaminant, stowaway	Allergic reaction	No
Baccharis halimifolia	Groundsel bush	Plant	North America	Europe, Australia	Escape	Allergic reaction	No
Heracleum mantegazzianum	Giant hogweed	Plant	Asia	Europe, North America, Oceania	Escape	Dermatitis	No
Opuntia spp.	Prickly pears	Plant	Central and South America	All other continents	Escape	Stings, painful dermatitis	No
Parthenium hysterophorus	Santa Maria feverfew	Plant	America	Australia, Asia	Contaminant	Painful dermatitis	No

collectors have developed eye inflammation and contact dermatitis in their hands and legs, to the point that some farmers have abandoned this practice in invaded regions (Shrestha et al. 2015).

18.4 Invasive Species Causing Allergies

18.4.1 Lepidoptera

The European gypsy moth, *Lymantria dispar dispar*, is native to Western Europe and has been introduced to North America. The Asian gypsy moth, *L. dispar asiatica*, is native to Southern Europe, Northern Africa, and Asia, but it is spreading to northwestern Europe where it hybridises with the European subspecies. In both cases, contact with the irritating hairs of egg masses and caterpillars, as well as the moth, may cause local dermatitis (erucism, lepidopterism) and also allergic reactions. This moth is listed among the 100 worst invasive species of the world (GISD 2015).

18.4.2 Plants

Many plants may adversely affect human health by releasing allergenic pollen into the atmosphere (Table 18.1). Allergenic pollen can cause conjunctivitis, rhinitis, and respiratory diseases such as asthma. Several non-native species are highly allergenic. In some areas the concentration of allergenic pollen from non-native plant species can be even greater than that from native species (Fig. 18.3). Moreover, because on average the flowering phenology of wind pollinated non-native plants is more advanced than in native plants, non-native plants extend the allergy risk period (Belmonte and Vilà 2004).

A main factor determining the concentration of airborne pollen is the high pollen production by certain species coupled with their high abundance (Fig. 18.4). Thus, even plants that have not escaped from cultivation (e.g., crops, gardens, landscaping) can cause allergy even if they have not naturalized. This is the case of ornamental trees from the Casuarinaceae, Cupressaceae, and Platanaceae families, which are extensively planted in urban areas and, even if their invasion potential is very low, the prevalence of their airborne pollen is very high. In Beijing, there is a strong correlation between non-native plant diversity and the frequency of allergenic plant occurrence (Mao et al. 2013). Urban planning should avoid introducing non-native species with allergenic pollen in parks, roadsides, and residential areas, especially in highly polluted areas, such as many Chinese cities.

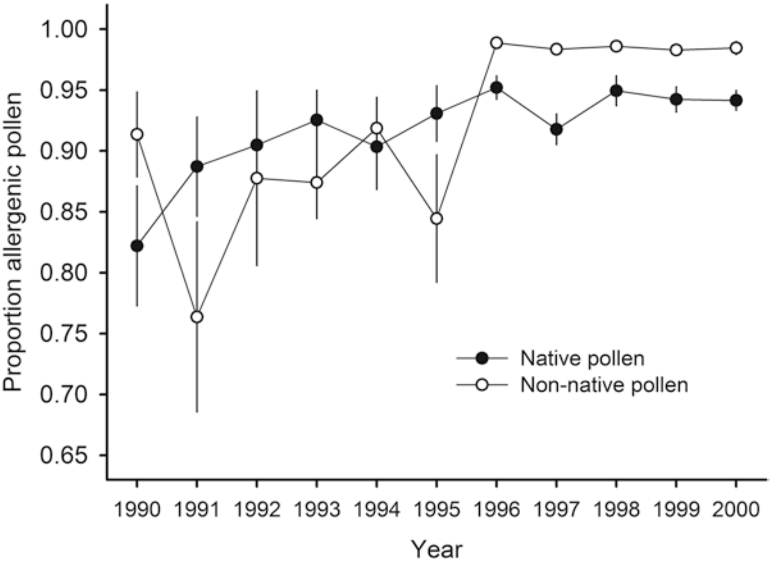

Fig. 18.3 Mean (±SE) proportion of native (24 taxa) and non-native (18 taxa) airborne pollen grains that are allergenic in five or six major cities in Catalonia. Sampling was conducted weekly by the Cour method from 1990 to 1995 and daily with the Hirst method from 1996 to 2000. The Hirst methodology gave low variation across sampling dates (Data from Belmonte and Vilà 2004)

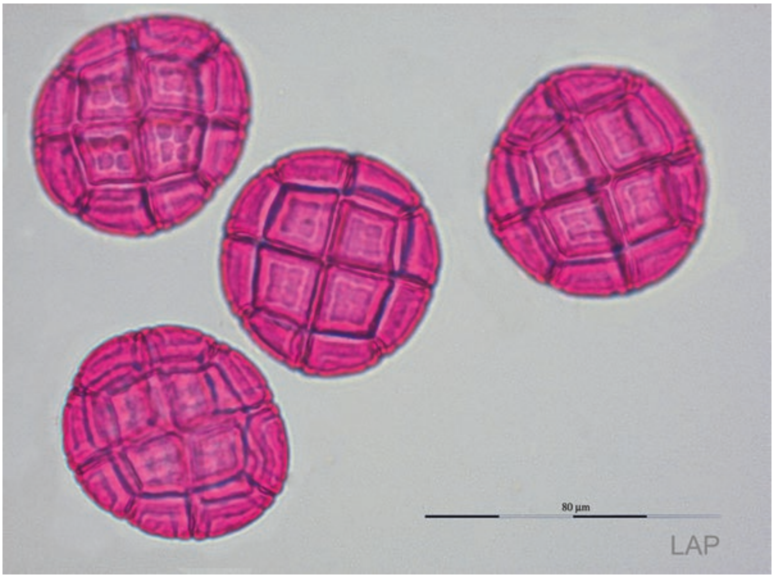

Fig. 18.4 Some non-native plants, such as *Acacia* spp., produce a high abundance of pollen that is allergenic to humans (Photograph by David Navarro)

One of the most studied allergenic invasive plant species is ragweed, *Ambrosia artemisiifolia*, an annual herb native to temperate North America that has been accidentally introduced in contaminated soil and grain in many parts of the world (Essl et al. 2015). In Europe, it is rapidly expanding its range with an average 10 % of Europeans being sensitised. In the past few years, there has been an increase in the incidence of allergenic reactions (Bullock et al. 2012). In Austria and Bavaria (southern Germany), it has been estimated that the medical costs caused by the allergic reactions produced by ragweed could reach by mid-century to €365 million annually in extreme climate warming conditions. Improved management focused on surveillance, early detection, and eradication programs are estimated to potentially reduce the monetary impacts on health costs to 43 % (Richter et al. 2013).

18.5 Invasive Species Causing Injuries

18.5.1 Mollusca

Because they have hard shells with sharp edges, dense populations of non-native mollusks can cause injuries to humans when walking barefoot on invaded coastal areas. An example is the American jackknife clam, *Ensis americanus*, native along the American West Coast and introduced, probably with ballast water, to the European Atlantic coast. Similarly, the zebra mussel, *Dreissena polymorpha*, a Ponto-Caspian species, has spread, via ballast water and ship hull fouling, to major parts of Europe and North America. This species is also listed among the 100 worst invasive species of the world (GISD 2015). The Pacific oyster, *Crassostrea gigas*, from the Pacific coast of Asia has meanwhile been introduced for aquaculture to America, Europe, and Australia and has frequently escaped to the wild.

18.5.2 Insecta

Mosquitoes can carry and transmit a number of pathogens that may cause serious health problems in humans (Rabitsch et al. 2017). Despite giving rise to several infectious diseases, the bites of these insects also cause skin irritations and sometimes intense allergic reactions. Very painful bites have been frequently reported in the case of the Southeast Asian tiger mosquito, *Aedes albopictus*, spreading to the Americas, Africa, and Europe. Most mosquitoes are nocturnal, but *A. albopictus* is diurnal, highly aggressive, and can eventually motivate people to avoid or leave certain locations (Gratz 2004). The stable fly, *Stomoxys calcitrans*, which is native to Eurasia but invasive in most other continents, is diurnal and may cause skin irritation leading to secondary infections.

18.5.3 Reptiles

The common caiman, *Caiman crocodilus*, is native to Central and South America and was originally introduced to Florida (USA), Puerto Rico, and Cuba for crocodile farming (skin and meat). However, when they escape, caimans can reach high population densities, for example, in Puerto Rico, where they have established in rural and even urban areas (Thomas 1999). However, they are relatively small and not aggressive, and their bites do not present a major danger to humans.

Boas and pythons are common in the pet trade, and individuals sometimes escape or are released by owners. The *Boa constrictor*, native to Central and South America, as well as the Burmese python, *Python molurus bivittatus*, are known to be establishing in south Florida, where they pose a serious ecological threat, but are of low risk to people, except, perhaps, to small children.

18.5.4 Plants

Contact with spiny non-native species, such as *Opuntia* spp., *Agave* spp., or *Ulex* spp., causes stings and skin rashes. They are a nuisance in leisure areas, or for environmental technicians or volunteers conducting manual removals (Fig. 18.5). Erect prickly pear, *Opuntia stricta*, and common gorse, *Ulex europaeus*, are listed among the 100 worst invasive species of the world (GISD 2015).

Fig. 18.5 Invasion by prickly pear cause stings and skin rashes. Plants are a nuisance in leisure areas, or for environmental technicians or volunteers conducting manual removals (Photograph by M. Vilà)

18.6 Conclusions

The majority of health impacts of invasive species concerns the transmission of pathogens or parasites to humans (Rabitsch et al. 2017), the bioaccumulation of noxious substances, the side effects of pesticide application to control these species, and increased health costs. Only a minority of non-native species raises human health problems as result of venomous stings and bites. A particularly dangerous situation results from mass attacks of social hymenopterans (bees, wasps, ants) when multiple stings occur, such as in the case of the Africanized honeybee. Astonishingly, those taxa which are famous for being venomous, such as scorpions and snakes, are of low importance as non-native species. The global invasive species database (GISD 2015) and the European database DAISIE (2015) do not list any non-native scorpion species, and most of the few non-native snakes mentioned are not venomous. Relevant marine species are generally found in only a few taxonomic groups (i.e., jellyfish, mollusks, fish). In the case of jellyfish, skin contact alone is sufficient to produce severe dermatitis. With regard to plants, the major health hazard is related to the allergenic pollen of wind-pollinated plants. Even introduced plant species, which have not escaped cultivation and are thus not naturalised (e.g. cypresses and ironwood), can be a health hazard for sensitised people.

Many of the species that have been introduced intentionally as pets (e.g., lion fish), as biocontrol agents (e.g., brown tree snake), or for ornamental purposes (e.g., gardening plants) arrive via pathways that are somewhat easier to manage by regulating trading and tenancy of species. However, many species are entering new areas as contaminants of traded goods or as stowaways (most insects). More effort to control these unintentional introduction pathways is urgently required to avoid further spread of non-native species with biological traits that cause human health problems.

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Chapter 19
Use of Non-native Species for Poverty Alleviation in Developing Economies

Arne B.R. Witt

Abstract For decades, development agencies, donors, and others have worked to improve the social and economic reality of people living in the developing world through inputs into the agricultural and fisheries sectors. To improve agricultural production and stem land degradation, often brought about by unsustainable land use practices, non-native tree and shrub species have been introduced, especially to Africa and Asia. To feed rapidly growing populations in these regions, non-native fish species have also been introduced to supplement existing protein sources, which are rapidly being depleted as a result of overexploitation and pollution. Many of these non-native species provide significant benefits to poor communities, but there are also costs associated with these introductions when species escape cultivation or culturing and establish populations in the wild. These "escapees" can have significant negative impacts on biodiversity and ecosystem function, negating their benefits, especially when measured at a landscape or national level. The failure of many development agencies and others to seek holistic or win–win solutions that benefit all sectors, or do not have negative impacts on others, will, in the final analysis, be to the detriment of the millions of poor communities they have tried to assist. The unfortunate reality is that many donors and development agencies have failed to recognise or acknowledge that cultured organisms can have significant impacts on ecosystems and human health should they escape and establish invasive populations.

Keywords Agro-forestry • Aquaculture • Developing countries • Livelihoods • *Pomacea canaliculata* • *Prosopis* species • *Tilapia* species

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19.1 Introduction

Ecosystem goods and services contribute directly to human well-being. These goods and services are critical to approximately 750 million of the more than one billion people living in rural areas. Most of these people live in absolute poverty, depend almost exclusively on natural resources, and are the most vulnerable when biodiversity is lost or degraded (MEA 2005). Poor rural people do not have alternative opportunities, and therefore the loss of biodiversity equates to a loss of "biological insurance" (MEA 2005). According to the Organisation for Economic Cooperation and Development (OECD), environment-based wealth accounts for about 25% of the total in poor countries, compared to less than 4 % in rich countries. As such, environmental degradation, especially in poor countries, has significant negative impact on rural communities that are dependent on the natural resource base for their survival.

Unsustainable land use practices, nutrient mining, deforestation, overexploitation, and land degradation have had devastating impacts on some of the most vulnerable people on the planet. In an attempt to halt or reverse further degradation, and to improve food production, a host of non-native species have been introduced that have, in many cases, benefitted rural communities and reduced pressure on natural ecosystems. However, many of these non-native species have proliferated outside cultivation, to the detriment of both the ecosystems and the millions of people who depend on them. This chapter considers some of the factors that are driving donors, development agencies, and governments to introduce non-native species, many of which have become established over large areas to the detriment of the natural resource base. Finally, some recommendations are made as to how this issue can possibly be addressed.

19.2 Drivers of Species Introductions

19.2.1 Lack of Soil Nutrients

Natural resources are under increasing pressure from overexploitation, largely driven by a rapidly expanding population and the demands of more affluent societies. It is predicted that we will need to feed a global population of about nine billion people in 2050, requiring raising food production by about 70 % between 2005–2007 and 2050 (FAO 2009). Food production in the developing world will need to almost double within that time, especially in sub-Saharan Africa, where we will see the highest population growth (FAO 2009). Given the strong link between soil fertility and food production, there will be a need to address soil fertility issues.

Soil nutrients can be replenished through the introduction of chemical or synthetic fertilisers and nitrogen-fixing plants. However, chemical fertilisers are generally too expensive for resource-poor farmers, and access is constrained by limited credit facilities and a lack of effective infrastructure for fertiliser production and distribution. As a result, nitrogen-fixing plants, many of them non-native, have been actively promoted in most of the developing world.

19.2.2 Fuelwood and Timber

Increased demand for fuelwood and timber is largely driving deforestation. Timber extraction and logging account for more than 70 % of total forest degradation in Latin America and tropical Asia, whereas fuelwood collection and charcoal production are the most important drivers of degradation in large parts of Africa (Kissinger et al. 2012). In many developing countries, wood-based fuels remain the dominant source of energy for more than two billion poor people. The absence of alternative sources of income, especially in urban areas, means that rural populations, mainly in Africa, continue to exploit forests and woodlands through shifting cultivation and charcoal production. One of the ways to reduce the use of native species, and to provide some protection to natural forests and woodlands, is to provide poor communities with alternatives, such as fast-growing non-native tree species. However, despite the introduction of non-native tree species, deforestation still continues throughout most of the developing world. Woodlots or plantations do “potentially” support natural forest conservation, but only marginally so, although the limited number of studies challenges any general conclusions (Secco and Pirard 2015). Many factors, including the respective locations of plantations and forests in relationship to the locality of households and villages, determine if woodlots or plantation are utilised in favour of natural forests (Secco and Pirard 2015).

19.2.3 Desertification

Deforestation is one of the activities that can contribute to desertification, which is largely driven by climate and human activities and results in increased soil erosion, decreased soil moisture, and soil salinisation. Desertification is common to drylands around the world, which occupy 41 % of the Earth’s land area and are home to about one third of the human population. It is estimated that desertification affects 70 % of all drylands, or 25 % of the Earth’s surface area, with more than 25 billion tonnes of topsoil lost annually (MEA 2005). Africa is particularly vulnerable to desertification as more than 60 % of the continent consists of desert or drylands. To halt or curb further desertification, a number of non-native tree and/or shrub species have been introduced.

19.2.4 Increasing Protein Production

As a result of unsustainable fishing practices most fish stocks around the world are in rapid decline. Water pollution has a significant impact on water quality, reducing the abundance of native fish stocks. Many rivers, reservoirs, and lakes in developing countries, especially in Asia, contain excessive amounts of bacteria from human waste and heavy metals, all of which contribute to eutrophication. Many freshwater systems are also highly stressed as a result of dam building, draining of wetlands, and excessive water abstraction. Poor water quality leads to a reduction in the availability of oxygen for aquatic plants and animals, which often stresses native species but can favour some non-native species that are often generalists and can survive in a wider range of conditions.

To mitigate against declining native fish stocks, development assistance programmes have largely focused on the introduction of non-native fish species. Most of these introduced fish species are reared commercially in pools, dams, or ponds and contribute significantly to protein production. Aquaculture currently accounts for nearly 50 % of the world's food fish consumption (FAO 2014). The perceived advantages of aquaculture include predictable availability of the resource, uniformity of the product in terms of age and size, and reduced stress and damage as compared to wild-caught fish. Aquaculture also has more efficient feed conversion rates than typical terrestrial animal farming and so provides a relatively cheap form of micronutrients to local communities (Gozlan 2017). Aquaculture can also serve as a source of supplemental income to rural farmers and communities.

However, many of these non-native fish species have escaped from rearing facilities and in some cases have also been introduced directly into the wild. Because development agencies have favoured non-native species that are generalists and exhibit rapid growth rates, many of these species have become widely established to the detriment of native fish stocks and other aquatic organisms.

19.3 Case Studies

There are numerous examples of non-native species that have been introduced into developing countries to improve opportunities for economic development. Unfortunately, the data available on these species are biased towards their potential economic benefits rather than adverse impacts. Although this can be attributed to a lack of research capacity in most of the developing world, it may also reflect a limited understanding by development agencies and recipient countries of the need to assess invasion risk and their failure to act on risk even when the potential environmental and socioeconomic consequences are conceptually recognised.

Agro-forestry trees and shrubs are typically selected based on their drought and salinity tolerance, rapid growth, yield in highly disturbed environments, and resistance to insect and disease attack. These are the same characteristics that predispose

Table 19.1 Number of tree species that were reported as naturalised or invasive outside their natural range, grouped according to economic use

	Forestry	Agro-forestry	Amenity	All purposes	Unclassified
Total number of tree species per sector	458	353	439	196	23
Species not reported invasive or naturalised	136	104	98	57	3
(% of total)	(30)	(29)	(22)	(29)	(13)
Naturalised and invasive species	282	203	292	114	15
(% of total)	(61)	(58)	(67)	(58)	(65)
Species that are naturalised only	40	46	49	25	5
(% of total)	(9)	(13)	(11)	(13)	(22)

Haysom and Murphy (2003)

a plant species to establish and proliferate in a new environment, often to the detriment of natural ecosystems. Similar criteria are used to select for fish and other animal species used to enhance protein production. It is, thus, not surprising that agricultural and forestry programmes are a major pathway for the introduction of a host of non-native species that have the ability to erode the natural resource base on which many people depend.

For example, a global review by Haysom and Murphy (2003) found that 443 woody non-native shrub/tree species (39 %) were introduced and invasive (i.e., species that were spreading unassisted or described as a non-native species that was thought to be in need of a control strategy). Comparatively, 74 (7 %) were introduced and naturalised (i.e., reported to occur in the wild, but not spreading) only, whereas 163 (15 %) were introduced and not naturalised or invasive. As such, 517 species (76 %) of non-native woody shrubs/trees were regarded as naturalised or invasive in at least one country or region (Haysom and Murphy 2003). These species are being used in forestry, agroforestry, or for amenity purposes with many allocated to more than one use category (Table 19.1). The region with the highest reported number of invasive non-native forestry tree species was Africa (87 invasive and 11 naturalised species) with the lowest number of invasions in Europe (12 invasive and 12 naturalised species) (Haysom and Murphy 2003).

19.3.1 *Shrubs and Trees*

Development agencies have largely favoured the introduction of multipurpose shrubs and trees that can provide fuelwood, building materials, animal fodder, mulch, and green manure, and can also be used to fix nitrogen, reclaim degraded

Fig. 19.1 *Prosopis juliflora* occupies thousands of hectares around Lake Baringo, Kenya, to the detriment of native plant and animal species and the communities that depend largely on natural resources (Photograph by Arne B.R. Witt)

wastelands, and retard erosion (Peoples and Craswell 1992). Shrubs and trees such as those in the genera *Prosopis*, *Leucaena*, *Acacia*, *Sesbania*, *Tephrosia*, *Morus*, *Crotalaria*, *Gliricidea*, *Gmelina*, *Calliandra*, and *Tithonia* have been widely promoted and utilised as multipurpose plants (Figs. 19.1 and 19.2). Other species in the genera *Eucalyptus*, *Pinus*, *Broussonetia*, *Cedrela*, *Maesopsis*, *Swietenia*, and *Tectona* generally do not have multiple uses and have mainly been promoted for timber and/or paper and pulp production in the commercial forestry sector, although they are often grown around rural homes or in small woodlots as a source of fuel and building materials.

The review by Haysom and Murphy (2003) found that 34 plant families contained more than one invasive tree/shrub species (Fig. 19.3), with more species in the genus *Acacia* (Leguminosae-Mimosoidae) reported as being naturalised or invasive than in any other group. At a global level, at least 23 Australian *Acacia* species are known to be problematic (Richardson and Rejmánek 2011), and many of these have negative impacts on ecosystems (Le Maitre et al. 2011) (Fig. 19.4). For example, in South Africa, costs associated with *Acacia mearnsii* infestations include reduced stream flows, a heightened fire risk, increased erosion, destabilisation of riverbanks, loss of grazing, and nitrogen pollution (de Wit et al. 2001). In Africa, outside of South Africa, *A. mearnsii* is the most widespread and abundant invasive

Fig. 19.2 The co-called "miracle" tree, *Leucaena leucocephala*, that was going to kickstart the green revolution in Africa, has failed to live up to its promise, forming dense stands in many areas to the detriment of biodiversity and ecosystem services (Photograph by Arne B.R. Witt)

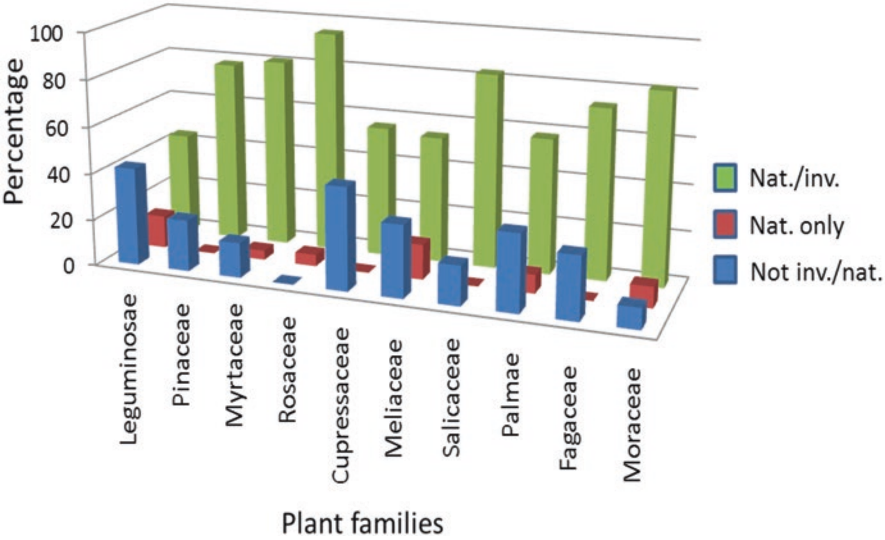

Fig. 19.3 The frequency with which non-native woody shrubs and trees naturalise or become invasive for ten major plant families: *inv* invasive, *nat* naturalised (From Haysom and Murphy 2003)

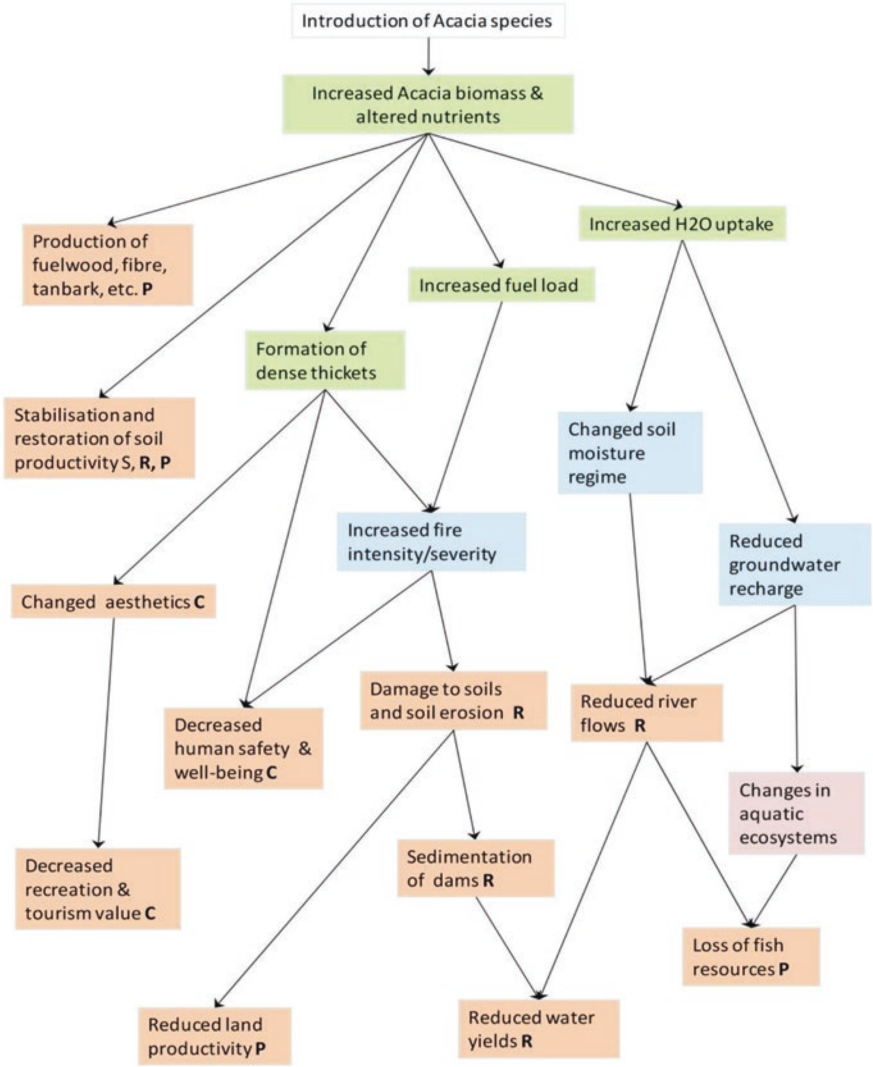

Fig. 19.4 A simplified cause-and-effect network diagram for introduced *Acacia* species shows selected biophysical impact (*green*, *blue*, *pink boxes*) and how they are linked and interact to affect ecosystem services in *orange boxes. S* supporting, *R* regulating, *P* production, *C* cultural (From le Maitre et al. 2011)

Australian *Acacia* species, followed by *A. melanoxylon* and *A. saligna. Acacia saligna* also increases nitrogen content of the soil, altering soil nutrient cycling; increases the intensity and frequency of fires; and reduces stream flows through increased water use, especially in water catchments (Le Maitre et al. 2000). In Asia, *A. mangium*, *A. auriculiformis*, and *A. decurrens* are known to have escaped cultivation, although the latter species is still restricted in its distribution. Because of lack of resources, little capacity, and a lack of awareness (Boy and Witt 2013), the total number of Australian acacias that are have escaped cultivation in Africa and Asia is unknown, but a considerable number have been introduced and continue to be promoted despite potential risks.

Other species introduced for afforestation in Africa (outside of South Africa) and Asia, mainly for timber and/or paper and pulp production, which are known or assumed to be having a negative impact on ecosystem services, include species in the genera *Pinus*, *Gmelina*, *Casuarina*, *Swietenia*, *Broussonetia*, *Maesopsis*, *Cedrela*, and *Tectona*. For example, *Pinus* species plantations in the KwaZulu-Natal Drakensberg, South Africa, reduced streamflows by 82 % (Bosch 1979) and contributed to the total drying up of streams 6–12 years after being planted. A similar impact was found for *Eucalyptus* and *Pinus* species in grassland catchments in Mpumalanga Province (van Lill et al. 1980). Although various *Eucalyptus* species are widely planted for timber and other uses in Africa, they appear to only occasionally escape cultivation outside South Africa.

Another group of species, better adapted to the more semiarid and arid parts of the world, have been introduced to curb land degradation and provide rural communities with alternative sources of fuelwood and fodder, and in some cases as a source of food. Species that have been widely promoted to curb desertification include various *Prosopis* species, *Parkinsonia aculeata*, and *Azadirachta indica*. Other species, such as *Acacia colei*, *A. torulosa*, *A. tumida*, and *A. elachantha*, also provide pods suitable for human consumption. However, many of these species are now considered to be having a negative impact on livelihoods and ecosystems. Dense stands of these, and other plant taxa mentioned, can have negative impacts on natural pest control, pollination, nutrient cycling, primary production, timber, nonwood products, genetic and ornamental resources, water purification and regulation, erosion control, livestock forage, air quality regulation, and recreation and tourism (Charles and Dukes 2007).

***Prosopis* Species** According to Pasiecznik et al. (2001), *Prosopis juliflora* and *Prosopis pallida* are two of the most “economically and ecologically important trees in arid and semi-arid zones of the world.” Various *Prosopis* species have been introduced to Africa over the past 200 years for their beneficial qualities, including erosion control, shade, fuelwood, building materials, and pods for animal and human consumption. Up to 70 % of the firewood needs of the rural poor in dry regions of India are now met by *Prosopis* species (Pasiecznik et al. 2001). The flowers are a valuable source of bee forage and the gum is of a very high quality. *Prosopis* species can also be a source of tannins, have some medicinal qualities, and provide shade for people and livestock.

However, *Prosopis* species are now naturalised in most countries to which they have been introduced, with millions of hectares occupied in the Sahel, East and southern Africa, South Asia, Southeast Asia, and Australia (Fig. 19.1). Initial assertions, that they would improve livelihoods, have not materialised (Mwangi and Swallow 2008; Maundu et al. 2009). The mean incremental water-use estimates of *Prosopis* species in South Africa were 33.2 m^3 ha/year for uplands and 212.3 m^3 ha/year for floodplains (Wise et al. 2012). It is also stated that *Prosopis* species are generally the "scourge of ranchers and pastoralists, but a boon to the rural poor" (Pasiecznik et al. 2001). Ironically, pastoralists are some of the poorest and most marginalised communities in the world. Communities in Ethiopia, Kenya, and elsewhere are increasingly concerned about the negative impacts of *P. juliflora* on beneficial native species; encroachment onto paths, villages, homes, water sources, croplands, and pastureland; and injuries from thorns causing animal and human health issues, apparently resulting in some human fatalities (see Nentwig et al. 2017). Surveys of local communities around Lake Baringo, Kenya, revealed that 85–90 % of respondents favoured complete eradication of invasive *Prosopis* species (Mwangi and Swallow 2008). In another study, Maundu et al. (2009) found that 64 %, 79 %, and 67 % of respondents interviewed in the Garissa, Loiyangalani, and Baringo areas of Kenya, respectively, said that life would be better without *Prosopis* species. More than 90 % of livestock owners in eastern Sudan regard invasive *Prosopis* species as a liability, and pastoralists in Ethiopia refer to *Prosopis* species as the "Devil Tree."

19.3.2 Aquaculture

A large number of non-native fish have been intentionally introduced to various parts of the world (Gozlan 2017). Examples include the notorious introduction of the Nile perch, *Lates niloticus*, which resulted in the extinction of many native cichlid species in Lake Victoria (Cucherousset and Olden 2011). Mozambique tilapia, *Oreochromis mossambicus*, has been introduced to 172 countries and established in 148, more than any other fish species (FAO 2014). Carp species have been widely introduced and established. For example, *Cyprinus carpio* has been introduced in 124 countries and become established in 53, *Ctenopharyngodon idella* has been introduced in 91 countries and become established in 10, and *Hypophthalmichthys molotrix* has been introduced to 79 countries and become established in 21; the Nile tilapia, *Oreochromis niloticus*, has been introduced to 78 countries and became established in 55 (FAO 2014). Of the 1205 fish introductions for aquaculture purposes, about 50% were followed by establishment in the wild (Casal 2006), and a large number of these have had significant negative impacts. Twenty-eight of the known crayfish species have established self-reproducing populations outside their native range and include several species perceived as problematic: Eastern crayfish, *Orconectes limosus*; signal crayfish, *Pasifastacus leniusculus*; common yabby, *Cherax destructor*; and red swamp crayfish, *Procambarus clarkii*. Non-native freshwater fishes can have ecological impacts at many different levels, including the genetic level (i.e., gene transcription and hybridisation), individual (i.e., behaviour, morphology, and vital rates), the population level (i.e., transmission of pathogens, acting as parasites, demographic effects, and distributional effects), the community level (i.e., species extinction, composition changes, alteration of food webs), and the ecosystem level (i.e., biochemical cycles, energy fluxes between ecosystems, ecological engineering) (Cucherousset and Olden 2011).

***Tilapia* Species** Tilapia, *Oreochromis* spp., cultured outside Africa reached 2.4 million tonnes in 2008, representing 8 % of all finfish produced outside Africa. Production of tilapia accounted for 34.7 % of the national aquaculture production in the Philippines, 19.5 % in Indonesia, 15.3 % in Thailand, 14.3 % in Malaysia, and 3.4 % in China (FAO 2010). Regions invaded by Mozambique tilapia include Japan, India, Indonesia, Sri Lanka, the Philippines, Guam, Papua New Guinea, Fiji, California, Mexico, Nicaragua, Venezuela, Madagascar, temperate parts of Africa (outside its natural range), and Australia (Hutchinson et al. 2011). Although tilapia mainly feed on detritus, algae, macrophytes, and other organic matter, they can shift their diet according to food availability, thereby transitioning from complete herbivory, to omnivory and total carnivory, and even to cannibalism. Non-native tilapia can cause changes in habitat through nest-building activities that increase water turbidity, uproot aquatic vegetation, alter erosion patterns, and decrease bank stability. The Mozambique tilapia has been implicated in the loss of native fish species in a host of waterbodies throughout its introduced range.

Three African tilapia species, including the Mozambique tilapia, were introduced into Lake Nicaragua in 1983 and 1984. By the early 1990s, the biomass of native cichlids declined by 80 % (McKaye et al. 1995). *Tilipia* species may now be edging out molluscivores from Lake Apoyo and have been blamed for an outbreak of blindness in native cichlids in Nicaraguan waters, caused by the introduction of a trematode infection.

In India, Mozambique tilapia adversely affected indigenous catfish, and in Powai Lake the introduction reduced the productive potential of the lake by 67 % (Bhagat and Dwivedi 1988). In one study in a Brazilian reservoir, catches over a 30-year period were significantly reduced for commercially important native species but increased for the introduced Nile tilapia, resulting in no overall increase in the productivity of the fishery as a whole. Elsewhere, fisheries have declined by between 67 and 80 % following tilapia invasion (Hutchinson et al. 2011).

Pomacea canaliculata The golden apple snail, *Pomacea canaliculata*, has been introduced as a human food source and is the hallmark of another food security project gone awry. At high densities, this herbivore can contribute to the complete loss of plants and may also contribute to the decline of native Asian freshwater snails, likely via competition. In the Philippines, it is considered the most serious pest of rice, with yield losses in affected areas increasing from approximately 2500 tons in 1985 to 25,000 tons in 1991 (Rice IPM Network 1991). The cumulative costs of *P. canaliculata* invasion, up to 1990, were estimated between US$425 and 1200 million (Naylor 1996). The golden apple snail is also a vector for the parasitic disease *Angiostrongyliasis cantonensis*, which causes eosinophilic meningitis in people.

19.4 Solutions

19.4.1 Wherever Possible, Use Local Species

There has been a tendency to "suppress interest in local species of possibly equal or greater value" (Welcomme 1984), because scientists have been more likely to promote those species they understand well rather than trying to domesticate lesser studied species. The dominance of non-native tree species in agro-forestry is largely attributed to the increased availability of technical and other information on non-native species and the abundance of and access to quality germplasm. There are also inherent risks in being dependent on a few species, creating a high likelihood of significant losses from a single disease outbreak.

There is also a general perception that all native species are slower growing and less productive or useful despite evidence to the contrary for many species. For example, the multi-purpose native African tree, *Faidherbia albida*, doubles or even triples maize yields when grown in fields in Niger, Nigeria, Burkina Faso, Mali, Senegal, Malawi, Zambia, and elsewhere. There are a large number of other native nitrogen-fixing species in Africa, including many *Acacia* spp., *Sesbania sesban*, *Brachystegia spiciformis*, *Crotolaria agatiflora*, and *Dichrostachys cinerea*, which can also be used for firewood, poles, medicine, soil conservation, and fibre. Native fodder species, such as *Alchornea cordifolia* and *Acioa barteri*, have the potential to be used in place of *Leuceana leucocephala* and *Gliricidia sepium* on acid soils in southeastern Nigeria (Cobbina et al. 1990).

These and other native species often have more uses than non-native species, and the fact that they have been used by communities for hundreds of years means that they are more readily accepted than non-native species and may also be important for local culture. The results of Farmer Managed Natural Regeneration (FMNR) have illustrated how beneficial the integration of native trees within an agricultural landscape can be. The integration/rotation of nitrogen-fixing food crops into cropping systems can also largely negate the need for the introduction of non-native nitrogen-fixing shrub or tree species.

19.4.2 Undertake Risk Assessments Including Cost–Benefit Analyses

In both the agro-forestry and aquaculture sectors, there has been a general failure to recognise the significant risks posed by non-native species. The lack of capacity or awareness has resulted in the introduction of species without adequate risk assessments being undertaken. It is critical that risk assessments be undertaken by the relevant regulatory authorities on all introduced species to prevent the introduction of potential non-native species. Ideally, these would be supported by cost–benefit analyses to evaluate whether the benefits associated with the introduction of a particular species outweigh any potential costs, especially in the long term. This information is critical because the demands on a non-native species may decline over time as an economy develops, and therefore the species may no longer be desirable or useful, leading to reduced use and as a result increased proliferation and spread.

Potential changes in land use and in climate also need to be evaluated as they may drive relatively benign species to become problematic. Any risk assessment should consider alternative species, especially native species, which may have slower growth rates but would have no associated potential costs. Evaluators also need to recognise that species that may not be considered as potentially invasive in one country or region may very well become invasive if introduced into a neighbouring area. If the risks of movement are high, measures need to be put in place to prevent the introduction of propagules elsewhere.

19.4.3 Make Information Readily Available

There is a dearth of information on which non-native species are present, their distribution, and what negative impacts they may be having on ecosystems and livelihoods in the developing world. A lack of capacity, awareness, and resources means that surveys are not undertaken, so it is not known which non-native species are naturalised or have negative impacts. Development agencies promoting these species often claim that the absence of records of invasiveness in a particular country or region are an indication that the species are not problematic, failing to recognise that this may be caused by a lack of capacity or surveys leading to the absence of information.

19.4.4 Introduce Host-Specific and Damaging Biocontrol Agents

Many introduced trees and shrubs have become problematic in Africa and Asia. South Africa, faced with a similar problem, has attempted to resolve the issue by introducing host-specific and damaging seed-feeding or flower-bud galling insects (Myers and Cory 2017). This method limits the further spread and densification of invasive plants without affecting the beneficial attributes of these species in terms of, for example, fuelwood production. Seed-feeding weevils in the genus *Melanterius* have been introduced for the control of the *Acacia* species *A. longifolia*, *A. melanoxylon*, *A. cyclops*, *A. dealbata*, *A. mearnsii*, and *Paraserianthes lophantha* (Moran et al. 2005). Flower-bud galling insects have also been introduced, effectively ‘sterilizing’ the plants. The introduction of host-specific agents that attack the reproductive parts of agro-forestry species which are known to escape cultivation and cause problems to biodiversity or human livelihoods should be a requirement for all development agencies promoting these species. Other options could include the introduction of sterile varieties, or using only male trees of dioecious species.

19.4.5 Reduce Demand

Unless the demand for timber, fuelwood, and other natural resources is significantly reduced, more and more non-native species will be introduced to compensate for the loss or reduction of native species populations. For example, to reduce the demand for energy from wood, it is critical that poor communities be provided with alternative options, especially those living in urban centres where the demand is highest. Without investments in alternative, clean, and cheap energy sources the demand for fuelwood will continue, leading to further land degradation, fuelling the demand for the introduction of additional non-native species.

19.5 Conclusions

Finding solutions to reduce or reverse land degradation and to enhance food production to feed a rapidly growing human population is a global challenge that will not be overcome by introducing species which have a negative impact on ecosystems or have the potential to do so. Although many non-native species provide significant benefits to poor communities, the costs associated with some of these introductions, if they establish populations in the wild, are significant. Individuals within one community may benefit while livelihood options for others may be considerably reduced. This conflict can only be resolved by developing holistic solutions that consider the potential implications of all interventions in all sectors and in subsequent years. Sustainable development is, after all, “development that meets the needs of the present, without compromising the ability of future generations to meet their own needs.” This regard is especially relevant when considering non-native species.

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Chapter 20
Non-native Species and the Aesthetics of Nature

Christoph Kueffer and Christian A. Kull

Abstract How humans perceive and judge nature and relate it to their life is shaped by emotional, cognitive, cultural, and social factors. Whether a species is considered native, non-native, or invasive can affect such aesthetics of nature by interacting with our emotions, affronting or confirming our cognitive categories, or engaging in our social, economic, and cultural worlds. Consequently, how humans perceive and judge the presence of such species, or how they judge an ecosystem or landscape change triggered by them, is not fixed or easy to define. Here, some of the psychological, cognitive, and social dimensions that influence how humans judge non-native and invasive species and their effects on ecosystems are reviewed. It is concluded, at least in the case of non-native species, that the reduction of aesthetics to a 'service' is problematic, for it occludes the complex psychological and social processes that shape divergent perceptions of changing species distributions.

Keywords Aesthetics • Cultural ecosystem services • History • Judgement • Landscape • Nativism • Perception • Political ecology • Psychology • Social • Valuation

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20.1 Introduction

The ecosystem services literature considers the aesthetics of nature to be a key cultural ecosystem service (Daniel et al. 2012). Non-native species can affect the aesthetics of nature by interacting with our emotions, affronting or confirming our cognitive categories and worldviews, or engaging in our social, economic, and cultural worlds (McNeely 2001; Hall 2003). They can contribute to, detract from, or simply alter the aesthetics of a particular nature.

How humans perceive and judge nature and relate it to their lives is shaped by emotional, cognitive, cultural, and social factors (Gobster et al. 2007; Daniel et al. 2012). This applies whether the 'nature' we are talking about is an individual plant or animal, a patch (a backyard, a trailside forest, or piece of species-rich lowland tropical forest), or a landscape (seen and appreciated from a viewpoint). In short, there is no such thing as a universal aesthetics of nature. How we see and relate to nature in its manifold forms lies in the eye of the beholder. Consequently, how humans perceive and judge the presence of species that are considered non-native or invasive, or how they judge an ecosystem or landscape change triggered by such species, is not fixed and easy to define. Here, the psychological, cognitive, and social dimensions that influence how humans judge such species and their effects on ecosystems are reviewed (Table 20.1). The terms perception (or to perceive) and judgement (or to judge) are used for describing the process of human evaluation of nature. Perception is used as a psychological term that refers to the ways in which humans filter, organise, and interpret information from the outside world; judgement more explicitly refers to the interpretive component, that is, how people assign values such as 'good' or 'bad' to aspects of nature.

Human perception and judgement are complex processes. We distinguish between psychological, cognitive, and social factors that can influence human perceptions of non-native and invasive species and their effects on ecosystems even though these three types of influences are necessarily intertwined (adapted from Kueffer 2013).

20.2 Psychological Factors

Our feelings towards a non-native species and its effects on the landscape can be shaped by the characteristics and 'reputation' of the species; by our reactions to landscape complexity or monotony; and by our perceptions of something being lost, such as a feeling of being at home in a place, or by our reaction to the rapid emergence of something new.

Table 20.1 Paradigmatic examples of complex, ambivalent, controversial, or changing perceptions of non-native species and their effects on landscapes, ecosystems, and society

Species	Description	References
Acacia spp.	Australian acacias have been introduced to many regions around the world for diverse purposes ranging from beautification to timber production. Uses and perceptions of acacias in particular regions have often fundamentally shifted in time, and often they have become an important part of cultural identity or livelihoods of some social groups while they are combatted as weeds or invasive species by others.	Kull et al. (2011)
Cinnamomum verum J. Presl.	Introduced to the Seychelles for spice production in the eighteenth century, in the nineteenth century, it colonized large parts of the deforested islands. Naturalized cinnamon restored forest cover and reduced erosion, and it supported for several decades a cinnamon industry that formed the backbone of the national economy. With the rise of nature conservation in the late twentieth century, it was considered the most problematic invasive plant species, while at present it is more often acknowledged as an integral part of novel ecosystems and local history with value for ecotourism.	Kueffer et al. (2013)
Echium plantagineum L.	A European herb introduced to Australia that was nicknamed "Salvation Jane" by dryland grazers and apiculturalists who appreciated it and "Patterson's curse" by farmers who despised it.	Cullen and Delfosse (1985)
Tamarix sp.	Saltcedar was introduced to the USA in the late 1800s and early 1900s to rehabilitate degraded land. Only a few decades later by the mid-1900s the species was combated because it was considered a problematic species negatively affecting water resources. Recently, some experts have portrayed the species once again more positively.	Stromberg et al. (2009)
Fish species	A long history of introducing fish to aquatic systems around the world led to a complex concept of what constitutes a non-native species integrating both biological and socioeconomic aspects.	Copp et al. (2005)
Sciurus carolinensis Gmelin	When controlling animal species such as grey squirrels, conservation of threatened native species can be in conflict with values of animal rights and welfare. In Italy, animal rights groups used legal means to prevent an eradication attempt of grey squirrels.	McNeely (2001)

(continued)

Table 20.1 (continued)

Species	Description	References
Myocastor coypus Molinathe	Introduced worldwide for fur production, in several places leading to local keystone industries, it is now often considered an invasive species. In some places it was at times protected by law because of overharvest. In Germany perception differed substantially between Western and former Eastern Germany. While it was considered a conservation problem in the West, it was of socioeconomic importance including as a source of meat in the East. There are organised supporters of the species in Germany, and material on, e.g., Youtube shows how it is perceived as an element of 'wild' and special nature in some cities. According to the IUCN red list it is considered threatened in some parts of its native range.	Carter and Leonard (2002)[a]

[a] http://www.nutria-info.com/gute-argumente-für-die-nutrias/

20.2.1 Charismatic Species, and Species with a Negative Image

There are species that have a positive image and others that have a negative one, and these judgements of particular species can be rooted in human psychology, but are also shaped through the lens of culture. Deliberately introduced non-native species are often brought to a new place because of some desirable aesthetic characteristics, for instance, 'cute' or 'charismatic' animals such as cats or rabbits (both considered problematic invasive species in some places) or plants with large and colourful flowers, such as the water hyacinth, *Eichhornia crassipes*. These positive characteristics can make it hard to explain to people why a problematic species should be removed (Fig. 20.1). Equally, some species have a bad image, which can add to or trigger negative perceptions of the species even when it might have no strong measurable negative ecological effects: it is easier to gain support for a black rat, *Rattus rattus*, eradication programme than efforts that target grey squirrels, *Sciurus carolinensis*, which, for instance, triggered opposition by animal welfare groups in Italy. In turn, it also matters whether the biota threatened by an invasion is charismatic or not. A control programme against non-native predators of endemic birds might get support, while the necessity to manage an invasion of earthworms affecting soil biota might be more difficult to communicate to a general public.

20.2.2 Monotony, Overabundance, and Loss of Diversity

Invasive species are represented by a wide range of taxonomic groups, forms, colours, and effects on landscapes and ecosystems. Thus, there is no generalisable effect on the visual appearance of an ecosystem or a landscape. There is, however,

Fig. 20.1 Coypu, *Myocastor coypus*, is widely considered an invasive species, but it is also appreciated as an attractive addition to the fauna and nature experience in cities such as Halle, Germany (Photograph by Sylvia Haider)

one general feature that is often considered to be associated with biological invasions (Humair et al. 2014b): this is the fact that they tend to lead to less diverse and more monotonous communities, ecosystems, and landscapes that are characterised by the abundance of a single or few species (Fig. 20.2).

How people perceive such landscape characteristics, and more specifically heterogeneity or monotony, is highly dependent on cultural contexts and expectations for a particular type of landscape, whether it is a wilderness area, rural agricultural landscape, or an urban place (Gobster et al. 2007). Historical cultural landscapes shaped by extensive land use, for example, are often appreciated for their heterogeneous mosaic (van Zanten et al. 2014), whereas monotony that triggers feelings of vastness or solitude might be appreciated in an Arctic wilderness area. Whether humans have an innate preference for certain types of landscapes, for instance, for those of intermediate heterogeneity and diversity, is an open research question (Ode et al. 2010). There is certainly not a general and undisputed dislike of monotonous landscapes; for instance, a spectacular bloom of one plant species, such as gorse (*Ulex europaeus)*, over an entire landscape can trigger feelings of natural wonder (Fig. 20.2).

Sense of Place There is no doubt that local nature can play an important role in helping people feel at home in a place, but the link between sense of place and the

Fig. 20.2 A landscape invaded by gorse, *Ulex europaeus*, on the Big Island of the Hawaiian Archipelago (Pacific Ocean) (Photograph by Eva Schumacher)

presence of non-native species is often not obvious (Humair et al. 2014b). One reason is that humans tend to adapt quickly to a new situation and often forget the nature of the past within a human generation or less ('shifting baseline syndrome'). For instance, in Madagascar, farmers considered non-native plants such as lantana, *Lantana camara*; Moluccan bramble, *Rubus alceifolius*; silver wattle, *Acaciadealbata*; and paperbark, *Melaleuca quinquenervia*; as normal, indeed 'native,' parts of the Malagasy landscape despite the fact that all were introduced. Very recent arrivals, however, were quickly noticed and evaluated for their utility or threat (Kull et al. 2014).

People will often consider the species that they grew up with as particularly important, whether they are unique native species, native species that profited from anthropogenic land use, or planted or naturalised non-native species (Humair et al. 2014b). Marris (2011) argued that when people grow up in novel ecosystems often dominated by non-native species, for instance, in urban or suburban areas, then such novel nature is the nature that matters to them; and it is such nature that they engage with emotionally and through their actions. This example also highlights that for understanding perceptions of change it is important to know what states people use for comparison. For instance, in the American Midwest, a flowering meadow of knapweeds, *Centaurea* spp., might be valued negatively if compared to a field of native sagebrush, particularly if the knapweed caused this change, but viewed positively if compared to an overgrazed and disturbed pasture, which may have enabled the knapweed invasion in the first place.

Another factor complicating the link between non-native species and sense of place is that we live increasingly in a time of rapid social change, widespread movement of people, and multicultural societies. Many people did not grow up in the places where they live today, and therefore today's local biota is not the same as they encountered in their childhood. In fact, it is often plants and animals from their previous homes, often non-native species, that help people to feel at home in a new and foreign place: this is one reason why people introduce non-native plants to new places (Daehler 2008).

Rapid Change and Novelty Invasive species can cause rapid ecological change. How people perceive such changes in their surroundings and their encounters with something novel has been studied by psychologists, including those working on risk. Novelty tends to be seen as risky and negative, although with exposure, people's risk perception and negative feelings tend to decrease (cf. Humair et al. 2014a). These reactions appear to be rooted in human psychology, relatively independent of culture. One mechanism that psychologists have identified is called 'mere exposure effect' (cf. Humair et al. 2014a). Humair et al. (2014a) showed that it was the novelty of a species, more than its non-nativeness, that led to increased perceptions of risk by horticultural practitioners in Switzerland. This effect decreased with the duration and intensity of interaction between a horticulturalist and a novel species. The opposite also held: horticulturalists tended to view non-native species that were important to their business as less problematic because they knew them well.

People differ in how they react to novelty. To use again the example of horticultural plants, novel plants might be valued highly because they are new, exciting, or something that others do not have, but people might also prefer plants that they have known for a long time because it generates a feeling of continuity, and assures them that they know how to grow the plants and how their friends will react to them. There are wide variations among people's perception of change and novelty. Although some prefer a cautious approach to ecosystem change, others favour experimentation in nature and will more positively value new species and landscapes (Gross 2010). This idea also implies that people think differently about approaches towards non-native and spreading species.

20.3 Cognitive Factors: Knowledge and Reasoning

Knowing and reasoning about the ecology and cultural significance of particular non-native species, their effects on ecosystem services, and available management options is important for shaping perceptions (reviewed in Kueffer 2013). A person who knows about specific negative impacts of a non-native species on native biodiversity will associate negative feelings with this species, even if it is beautiful. It has been shown that the role of knowledge is stronger when this comes from personal experiences with problematic aspects of an invasive species, but also more general knowledge ('competence') about non-native species, nature, and nature conservation can influence perception of non-native species (Fig. 20.3).

However, it is important to recognise that knowledge is relative: it can be strongly influenced by worldviews, values, and the workings of institutional power.

Fig. 20.3 Pillar Rocks, a tourist attraction in the Palni Hills of southern India. Non-native black wattles, *Acacia mearnsii*, planted on montane grasslands for tanbark now contribute to visitor satisfaction but pose challenges related to their invasiveness (Photograph by Christian Kull)

Knowledge is often transported through value- and power-laden concepts, categories, and metaphors (Kull and Rangan 2015; Kueffer and Larson 2014). We discuss some of these notions here.

20.3.1 Invasive Species and Biological Invasions

How the spread and presence of novel species, and the change induced by them, is represented in language, metaphors, stories, and visualisation affects how people perceive them and the resulting landscapes. In this context, the use of notions such as 'invasive' or 'invasion' has been amply discussed (Kull and Rangan 2015; Kueffer and Larson 2014; Larson 2005). Labelling a new species spreading in the landscapes as 'invasive' gives rise to different perceptions than saying that the species is 'extending its distribution.' The rhetorical framework of 'invasion' can for instance wrongly give the impression of rapid change, when a biotic change might actually have happened over long time periods, and on the other hand can move attention away from more incremental, but equally fundamental, changes.

20.3.2 Native and Non-native

Another key concept is the nativeness or non-nativeness of a species. Beyond being a concept used by scientists, this is also a notion that has a long and diverse cultural history, often tied to ideas of nationalism (Hall 2003; Kull and Rangan 2015). The concept of a non-native or native species can differ substantially between different experts, the public, and experts, and among different social groups or individuals (Humair et al. 2014b). The cultural history of the notion influences how humans perceive non-native species, and these influences can differ depending on which term is used, whether alien, adventive, exotic, foreign, introduced, neobiota, non-indigenous, or non-native. Even if scientists attempt to use the term 'native' only with a specific and 'scientific' meaning, they cannot neglect that the connotations of the term in a particular cultural context will influence how people think about 'non-native' species and perceive and value them in the landscape.

20.3.3 Wilderness, Concepts of Naturalness and Ecological Order, and the Perceived Role of Humans in Nature

How people perceive a landscape, and the species in this landscape, depends on the expectations people have for this landscape (Gobster et al. 2007). When it comes to valuing 'natural' landscapes it matters how people think of nature, what their concepts of naturalness are, and how they perceive the role of humans in nature (Fischer and van der Wal 2007; Carlson and Lintott 2008). For instance, people may differ in their understanding of how nature is organised, whether it is in a stable balance or in constant flux, or whether it is well ordered or chaotic. Novel species and associated changes will be perceived more positively by those people that see nature as something constantly changing than by others who hold on to the ideal of balance of nature (Fischer and van der Wal 2007). The idea that integrity, stability, and balance are defining characteristics of 'pristine' nature (i.e., nature not influenced by humans) has been very influential in the Western context. Aldo Leopold, one of the pioneers of twentieth-century nature conservation in the USA, for instance, attempted to develop an aesthetics of nature's beauty that built on the perceived special qualities of ecosystems shaped by long-term coevolution and ecological ordering. Leopold's aesthetic is more about a sophisticated, cognitive appreciation of these qualities than about visual beauty (Callicot 1983). Leopold also referred to introduced species as a threat to such order and thereby exemplifies a view that sees introduced species as disturbing the integrity of ecosystems and thereby their beauty (reviewed by Simberloff 2012).

The concepts of wilderness and wild nature are also particularly important. Wilderness, in its current dominant usage in the context of biological conservation, generally refers to areas where humans (and their influences) are absent. But it is important to acknowledge that concepts of wilderness often vary between sociocultural contexts, change with time, and are very much a human-created idea (Cronon 1996). Today, the wilderness is often seen as an idyllic place, contrasting with a noisy and stressful daily life in a modern civilisation, and associated with positive but strongly contrasting ideas, such as vastness, frontier, adventure, solitude, or exotic places. In contrast, in the past, the wilderness was often associated with negative feelings, such as danger of wild animals, bandits, or lack of shelter from dangerous weather events. Correspondingly, 'wild' still today stands for dangerous, unplanned, unmanaged, unpredictable, or chaotic. The 'wilderness' concept is important in the context of non-native species, because non-native species are often considered to be species that are brought to a new place through human agency and therefore turn wild places into nature touched by humans. However, the self-propagated expansion of a novel species into a natural area can add 'wildness' in the sense of unpredictable and unplanned processes, whereas the planned control or eradication of a non-native species in a wilderness area brings an element of design to an area not meant to be shaped by humans. The wilderness concept thus touches upon underlying paradoxes that guide peoples' perceptions of non-native species.

20.4 Social, Economic, and Historical Factors

It is crucial to understand human perceptions of non-native species, their effects, and their management in their particular social and economic contexts, shaped by the particularities of geography and history at multiple scales (Kull et al. 2011).

Peoples' perceptions are shaped by economic interests, cultural traditions, symbolic representations, social relationships, and other factors that are difficult to understand outside the local, regional, or national context.

An obvious factor is the utility or nuisance of a non-native species in particular landscapes. People who profit from the presence of a species will perceive it differently from those whose economic activities are negatively affected. A classic example is *Echium plantagineum*, a European herb introduced to Australia that was nicknamed "Salvation Jane" by dryland grazers and apiculturalists who appreciated it and "Patterson's curse" by farmers who despised it (Cullen and Delfosse 1985).

Values related to non-native species are also rooted in the history or culture of a society. Some non-native species play, or played in the past, an important role in the culture of a society, for instance, the candlenut tree, *Aleurites moluccana*, introduced by Polynesians to Pacific islands. The appreciation of silver wattle, *Acacia dealbata*, in France reflects its now long-term association with the landscapes of the Côte d'Azur despite evidence of invasion.

Ideas linked to nationalism can also influence the perceptions of 'native' and 'non-native' species. In nineteenth- and early twentieth-century Germany, the promotion of native plants in landscaping was strongly associated with nation building. In settler colonies, such as Australia and South Africa, the identification with 'indigenous' flora and fauna from the new place, as well as familiar land use systems with their associated biotas transported from Europe, served in building a new national identity. In such cases, nationalistic ideas can accentuate negative or positive perceptions of either native or non-native species.

Any human judgement is influenced by broader concepts that are culturally rooted and value laden, but this entanglement of personal affection and culture might be particularly tight and dynamic in the case of biological invasions. This connection occurs because the terms non-native and invasive have strong connotations and a rich history, and biological invasions also interfere with some of the most fundamental ideas about human relationships with nature, such as wilderness, cultural heritage, 'pristine' nature, or balance of nature. In modern societies, science has a strong influence on the production and reception of such notions, and consequently changing evaluations of non-native species are often the result of a tight entanglement of changing expert paradigms and evolving social and cultural views (that can be the result of shifts in power relationships) (Stromberg et al. 2009). Saltcedar, *Tamarix* spp., for instance, was introduced to USA in the late 1800s and early 1900s to rehabilitate degraded land. Only a few decades later, by the mid-1900s, the species was combatted because it was considered a problematic species negatively affecting water resources. Recently, some experts have portrayed the species once again more positively (Stromberg et al. 2009). Similarly, views of German foresters towards black cherry, *Prunus serotina*, varied over time and with forestry practices and scientific advice. Their perceptions were initially based on their hopes for timber or soil improvement, later on their fears about invasion, and then on their hopes for mitigation and living with the species (Starfinger et al. 2003). These discourses were only partly based on facts.

Social factors and social relationships have recurrently been shown to affect the perception and judgement of non-native and invasive species (reviewed in Kueffer 2013). The socioeconomic or demographic background of a person matters, and so too does the social or interest group to which a person belongs. For instance, tourists, nature conservation managers, or local residents can differ in their perception. In Australia, rivalry between community groups that competed for funding and media attention to combat cane toads, *Rhinella marina*, affected support of control measures against the species (Shine and Doody 2011). In summary, the perception of the aesthetics of landscapes and their biotas often cannot be separated from the social relationships of those that live in the landscape or from the history of human-nature relationships in a place.

20.5 Aesthetics of Nature—An Ecosystem Service?

Aesthetics and other categories of ‘cultural ecosystem services’ have always been difficult to integrate into ecosystem services conceptualisations because of their subjectivity, intangibility, and non-quantifiability (Daniel et al. 2012). Non-native species clearly have effects on the subjective and relative characteristics of aesthetics. An underlying assumption of applying the ecosystem services concept to biological invasions is that the provision of these services changes through the effects of non-native species on the biology and ecology of the place. Yet, the cultural service of aesthetics cannot simply be said to ‘exist’ in physical space when its character is so much in the eye of the beholder and his or her cultural and social context. Certainly the presence of ‘nature’ gives people something to behold, but the appreciation and judgement of aesthetics is a complex human psychological and social endeavour that is partly independent of biophysical changes to this nature.

Such interpretative fluidity is a challenge for the ecosystem services conceptual system as well as for environmental management. Yet the difficulty of fitting aesthetics into the rubric of cultural ecosystem services, and the lack of immediate management consensus on non-natives from an aesthetic aspect, also has a flip side: the fact that perceptions of aesthetics are relative and socially influenced, which opens up space for shaping such perceptions through advocacy. Notions such as ‘non-native’ and ‘invasive’ have in the past been used strategically to bring actors together behind a common cause. Yet such rhetorical strategies have been criticised because they build on problematic, violent, and exclusive discourses (Larson 2005). There is little doubt that conservationists should highlight the values of past and current nature and warn of the risks posed by some non-native species to the ecological functioning and the uniqueness of ecosystems. Such advocacy will however only be effective if it engages with the psychological, social, and cultural relationships that people have with their surrounding nature. The normative views that are implicit in a conservationist way of representing ‘biological invasions’ must be made explicit, thereby opening them to transparent deliberation (e.g., Kueffer and Larson 2014; Kueffer and Hirsch Hadorn 2008; Gobster et al. 2007).

20.6 Conclusions

There are psychological, cognitive, and social dimensions that influence how humans judge non-native and invasive species and their effects on ecosystems. It is concluded, at least in the case of non-native species, that the reduction of aesthetics to a ‘service’ is problematic, when its character is so much in the eye of the beholder and his or her cultural and social context. The cultural service of aesthetics cannot simply be said to ‘exist’ in physical space. Rather, how humans relate to non-native species is part of an entangled and dynamic web of psychological factors, interests, social relationships and cultural views of plants and animals, of landscapes, of nature as a whole, and of the place of humans in nature.

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Part V
Synthesis

Chapter 21
Integrating the Impacts of Non-native Species on Ecosystem Services into Environmental Policy

Philip E. Hulme and Montserrat Vilà

Abstract As momentum increases to apply ecosystem service perspectives to a wide range of environmental and conservation-related policy issues, it is increasingly important that this approach be applied to the prevention and management of harmful non-native species. A tiered approach can be applied that first recognises the value of the ecosystem service at risk from non-native species, subsequently demonstrates the impacts quantitatively, and finally captures these impacts through the introduction of mechanisms that incorporate the values of ecosystems into decision making. A few risk assessment approaches follow this tiered approach but as yet do not capture the complexity of ecosystem service impacts generated by non-native species. The absence of quantitative ecological and economic data on the impacts of certain ecosystem services limits the development of regulatory initiatives. Most non-native species introduced by humans have value to one or more sectors of society. As a result, conflicts arise in the estimates of the net value of non-native species to ecosystem services. A series of scenarios are used to illustrate how the strength of such conflicts might vary under different circumstances and what options might exist to achieve resolution. Addressing the impacts on ecosystem services will require understanding of environmental conflicts and policy tools that can better capture impacts of commercially important non-native species. Conflict resolution may involve management rather than eradication of a particular non-native species if this species proves to be appreciated by certain stakeholders. Alternatively, a polluter-pays principle could require those introducing non-native species internalise the costs of any subsequent environmental impacts.

Keywords Alien • Conflict resolution • Exotic • IPBES • Pathogen • Pest • Risk assessment • Service providing unit • TEEB • Valuation • Weed

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21.1 Introduction

The ecosystem services concept is a particularly useful framework for policy makers for its inclusive nature. It encompasses all environmental compartments (aquatic, terrestrial, and atmospheric systems), ecological entities (species, communities, habitats) across all taxa (flora, fauna as well as microorganisms), and covers the potential consequences of different human uses of ecosystems (e.g., production and conservation). As a result it has been adopted for different purposes by environmental bodies. The United Nations Environment Programme (UNEP) supports the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), an independent intergovernmental body established to strengthen the science–policy interface for biodiversity and ecosystem services. UNEP is also a partner in the Economics of Ecosystems and Biodiversity (TEEB), a global initiative focused on "making nature's values visible" (Ring et al. 2010; Schmeller and Bridgewater 2016). However, despite these global initiatives the application of an ecosystem service approach to support policies targeting non-native species is still in its infancy.

A key component in both TEEB and IPBES is the valuation of ecosystem services. In general, ecosystem services have been described in relationship to the extent they have explicit prices or can be traded in an open market. Provisioning services (such as crops, livestock, fish, water) that are consumed by people have *direct-use values* for which there is a long history of explicit pricing, whereas regulating and supporting services (including water purification, climate regulation, and pollination) have *indirect-use values* which have only recently begun to be assigned an economic value. Cultural services, while often influential in decision making, have *non-use values* whose benefits have only rarely been explicitly valued in monetary terms. There remain relatively few studies that have quantified direct-use, indirect-use, and non-use values of the ecosystem services impacted by non-native species (Born et al. 2005)

Policymakers applying an ecosystem services approach to managing the environment are recommended to follow a tiered approach to assessing the value of ecosystem services (TEEB 2011). Initially, the *value* of the ecosystem service has to be recognised. This process may be straightforward for tangible services that have direct-use values (food, fuel and fibre crops) and even non-use values when these are captured in legislation (e.g., protected areas). However, indirect-use values are often less tangible (e.g., nutrient cycling, water purification), which also reflects the state of scientific knowledge regarding regulating and supporting services. Once recognised, the value of a service needs to be *demonstrated*, often in economic terms. There are a number of different economic valuation methods, all of which have advantages and disadvantages (Williams et al. 2010). Nevertheless, there are three important aspects that need to be borne in mind when valuing ecosystem services: (1) the full costs and benefits of a proposed use of an ecosystem have to be estimated; (2) not all biodiversity values can be reliably quantified using existing methods; and (3) the tools are best applied for estimating the costs and benefits of changes to ecosystems rather than absolute valuation of the ecosystem. As a result, the full range of ecosystem services is rarely assessed and studies usually focus on just a few services. Finally, the values of ecosystem services have to be *captured* into policy, which involves the introduction of mechanisms that incorporate the values of ecosystems into decision making, through incentives and price signals. However, when addressing multiple ecosystems, services or cultures monetary incentives and tools may be less reliable or unsuitable.

It should be noted that this approach to valuing ecosystems has been the subject of at least four major criticisms (Melathopoulos and Stoner 2015). First, the process of abstracting services from ecosystem functions obscures the complicated interconnections within ecosystems and between society and ecosystems. Thus, social benefits arising from ecosystems cannot be captured through a single dimension that involves the quantitative and objective measure of individual consumer preferences. Second, although ecosystem service values are taken to be an objective measure of social welfare, they in fact often represent the narrow interests of environmentalists or scientists who extend their objective ecological findings to questions of social necessity. Third, the overwhelming demand for some services (e.g., carbon sequestration) can lead to the degradation of other associated ecosystem services (e.g., habitat quality for wildlife). Fourth, from a pragmatic perspective, ecosystem service valuations only protect biodiversity if it is threatened with destruction or where there is no alternative that will provide as cheap and as good a substitute. It therefore serves no purpose to place a value on services that are not threatened, because if the services are plentiful and free their economic value is zero, no matter how beneficial they might be. These criticisms apply to any attempt to value ecosystem services but are particularly germane when addressing the impacts of non-native species. Non-native species affect a wide range of ecosystem services both negatively and positively such that approaches that examine only a single dimension are liable to fail. Similarly, scientists studying biological invasions have been criticised for overselling the problem to secure long-term research funding to support their own particular concerns and interests (Simberloff 2015). Finally, many studies of the impacts of non-native species do not address the threat to endangered species or protected ecosystems (Hulme et al. 2014).

This chapter explores the utility of the ecosystem framework for advancing policies targeting the risks posed by non-native species. Using the tiered approach proposed by TEEB, the challenges facing social and natural scientists as well as policymakers are examined in the light of available data on non-native species impacts and the implicit criticisms facing the ecosystem service approach to biodiversity conservation.

21.2 Risk Assessment of Ecosystem Service Impacts of Non-native Species

An important aspect of policymaking in relationship to the problems posed by non-native species is the development of a robust mechanism to assess risks to support regulatory activities in an objective and transparent manner (Hulme 2011). Given the considerable evidence that non-native species can have major impacts on ecosystem services, there is substantial scope for integrating an ecosystem service perspective within a risk assessment framework. Although there are several different approaches to addressing the risks posed to an ecosystem by non-native species (Blackburn et al. 2014; Ojaveer et al. 2015), attempts to include an explicit ecosystem service focus have only recently been developed (Gilioli et al. 2014; EFSA 2014).

21.2.1 Defining the Ecosystem Services at Risk

The first step in assessing the risk posed to ecosystem services from one or more non-native species is identifying the ecological entity (e.g., species, community, habitat) and attributes (e.g., survival, population density, species richness, primary productivity) that are threatened by invasion. This approach is equivalent to the policymaking step of demonstrating *value*. Quantitative information on how specific ecosystem functions are impacted by non-native species are often collected through field studies, but both the spatial scale and range of variables examined are often fairly limited. Furthermore, the impacts on individual ecosystem functions are rarely integrated in a sufficient way to indicate how ecosystem services might be altered (Hulme et al. 2013). As a result, the inferences regarding ecosystem services can be difficult.

Alternative approaches may assess impacts indirectly by characterising changes to either service-providing units (SPUs) that explicitly link species populations with services or key ecosystem service providers (ESP) which characterize the key traits and functional importance of populations, communities, guilds, and interacting networks of organisms that deliver services (Luck et al. 2009). Although conceptually elegant, identification of an SPU or ESP is rarely straightforward and usually involves the identification of functional groups within the fauna and flora that are important to ecosystem service delivery. One problem is that although functional traits are known to underpin species contributions to ecosystem services, the interpretation of shifts in functional composition in relationship to changes in service provision are complex (Lavorel and Grigulis 2012). The simplest case would be of an introduced fungal pathogen reducing the performance of a single crop species with resulting loss in yield and financial returns to farmers (Fried et al. 2017). Here, the crop is clearly the SPU/ESP and both the vulnerability and consequences of the introduced pathogen can be quantified. A more complex scenario is one in which the non-native species, for example, a highly attractive non-native ornamental plant species, impacts on one element of a guild of SPU/ESP, such as pollinating insects. In this case, the relationship between an ecosystem service (pollination) and the impact of a non-native species is unlikely to be 1:1, because even if the guild structure or activity of pollinators changes, there may still be compensatory effects among pollinators such that pollination services are only weakly impacted (Morales et al. 2017).

Recent risk assessments have treated entire ecosystems as the SPU/ESP. In the case of the golden apple snail *Pomacea maculata*, the SPU is described as being "*shallow fresh water areas containing macrophytes such as wetlands, shallow lakes, river deltas and the littoral zone of deeper lakes and river*" (EFSA 2014), whereas for the citrus long-horned beetle, *Anoplophora chinensis*, these were defined as "*urban areas and those in more complex environments such as orchards and natural woodland*"(Gilioli et al. 2014). As impacts may be strongly context dependent, such broad-scale definitions of SPU/ESP suffer from a lack of internal homogeneity and a level of complexity that may be hard to quantify. As a result, the assessment of the impact of these two pest species on ecosystem services do not formally characterise the functional diversity of the ecosystems affected nor how they might change following invasion (EFSA 2014; Gilioli et al. 2014). Given the limited quantitative data on non-native impacts on ecosystem services (Hulme et al. 2013; McLaughlan et al. 2014), considerable work is required to ensure the magnitude of impacts on ecosystem services are adequately estimated.

21.2.2 Assessing the Magnitude and Scale of Ecosystem Service Impacts

Demonstrating the value of the services at risk requires quantification of the magnitude of actual or potential impact by a non-native species on the SPU/ESP. The effect can be either direct, such as non-native freshwater cyanobacteria releasing potent toxins contaminating drinking water (Costa et al. 2017), or indirect, as in the case of non-native crazy ants, *Anoplolepis gracilipes*, on Christmas Island that by extirpating the red land crab indirectly slowed litter breakdown (O'Dowd et al. 2003). Indirect effects require far more understanding of the consequences of an invasion on food webs and the trophic structure of ecosystems (Walsh et al. 2016). It is important to note that the effect of a non-native species may be either a decrease or an increase in a particular ecosystem service (Pyšek et al. 2012), and thus any quantification of impact should account for both potentially positive and negative consequences for human well-being. A key issue is whether only negative impacts should considered when assessing the risk of non-native species on ecosystem services. Such an approach would run contrary to the philosophy of ecosystem service valuation that attempts to balance costs and benefits. The counterargument is that non-native species of high economic value, such as crops, would be viewed as having a net benefit despite considerable impacts on biodiversity: this will often be the case because of the difficulties of valuing nature or cultural significance of species and ecosystems. For example, in New Zealand the Monterey pine, *Pinus radiata*, has spread from plantations to invade natural areas, yet its value as a forestry crop amounts to more than US$10 billion. It might therefore be expected that by valuing this provision service so highly foresters could argue that this would offset the considerable negative impacts on other ecosystem services.

The temporal and spatial scales at which impacts are assessed are also important. Few ecological studies examine impacts of non-native species at large enough spatial scales or on long enough temporal scales to adequately quantify consequences for ecosystem services. These dimensions are interdependent in that some impacts can be absorbed by an ecosystem over a short time scale but may result in irreversible effects if they continue over a long time scale. Similarly, a small impact on population density of an endangered species may have limited effects if it occurred on a local scale for a medium period of time, so long as on a regional scale the population is not affected (Blackburn et al. 2014). Attempts to scale up from plot data to regions have focused on regulating services, such as water availability, or provisioning services, such as crop yield. These methods use plot data to provide an estimate of the average impact and then apply either the current and/or future potential distribution of non-native species to estimate the large-scale consequences for ecosystem services (Le Maitre et al. 2015; van Wilgen et al. 2008; Williams et al. 2010). Scaling-up impacts of cultural services may be more challenging because of the complex context dependence of socioecological systems that lead to perceptions of non-native species varying among regions (Witt 2017).

21.2.3 Capturing the Economic Value of Non-native Species on Ecosystem Services

The total economic value of an ecosystem service includes its direct-use values, indirect-use values, and non-use values. To date, most estimates of the economic cost of non-native species have focused on direct costs, and usually only the direct costs associated with management expenditure on prevention, control, and eradication (Born et al. 2005; Williams et al. 2010). Yet from an ecosystem services perspective, it is the direct costs linked to the alteration of the service (e.g., decreased crop yields or water quality) that are important to quantify.

To examine how costs might vary across different ecosystem services and how they might compare to management costs, data have been extracted from an economic analysis of costs of non-native species in Great Britain (Table 21.1). An immediately obvious trend is that the ability to quantify impacts differs across ecosystem services. Impacts on provisioning services are most easily estimated whether it be through yield losses in grassland (rabbits) or timber (green spruce aphid, grey squirrel, red needle blight) production, predation on livestock (mink feeding on poultry), or reduced honey yield (varroa mite).

In contrast, there are no monetary estimates of the costs of non-native species to supporting services such as nutrient cycling, carbon sequestration, hydrology, and changes in habitat composition. Non-native species can transform native habitats in Britain. *Rhododendron ponticum* dramatically changes the appearance of open heathlands and the understory of Atlantic oak woods, yet the complexity of this ecosystem transformation in terms of loss of habitat has hindered any monetary valuation (Williams et al. 2010). There are also relatively few monetary

Table 21.1 Estimated monetary value of selected non-native species on ecosystem services in Great Britain compared to expenditure on their management

Species	Common name	Ecosystem service value (£M)				Management costs (£M)
		Provisioning	Regulating	Supporting	Cultural	
Hydrocotyle ranunculoides	Floating pennywort				23.54	1.93
Varroa destructor	Varroa mite	1.37	13.68			4.44
Oryctolagus cuniculus	Rabbit	183.28				4.34
Neovison vison	Mink	0.14			2.54	0.79
Sciurus carolinensis	Grey squirrel	0.68				5.41
Elatobium abietinum	Green spruce aphid	3.57				–
Dothistroma septospora	Red band needle blight	0.76				–
Pacifastacus leniusculus	Signal crayfish		0.20		1.00	1.30
Buddleia davidii	Buddleja				0.610	0.35

Values are in £ millions and taken from Williams et al. (2010)

estimates of impacts on regulating services (Table 21.1). The largest impact is that attributable to the varroa mite on pollination services. Yet even this value may need to be interpreted with caution because it is based on an estimate of the percentage of honeybee, *Apis mellifera*, hives destroyed as a result of mite infestation. Approximately 7 % of hives might be lost to varroa (Williams et al. 2010) but whether this results in a significant decline in pollination service depends on the extent to which this decline in hives reduces crop pollination by a similar amount. If there were to be competition among beekeepers for the provision of pollinators to farmers, then a reduction in hives may simply reduce this oversupply. The only other regulating service for which there is an estimate is for the cost of restoring erosion damage to riverbanks as a result of burrowing by signal crayfish (Table 21.1). It is likely that riverbank erosion would also arise from the burrowing behaviour of the Chinese mitten crab, *Eriocheir sinensis*, but no estimate of this impact exist. Similarly, an important omission in estimates of impacts on regulating services would be those attributable to the zebra mussel, *Dreissena polymorpha*, which is known to affect water quality in Britain (McLaughlan and Aldridge 2013).

Impacts on cultural services include the damage to heritage buildings caused by buddleia; mink preying on the protected water vole *Arvicola amphibius*, and the loss in recreational resources on waterways either because floating pennywort impedes boating or signal crayfish disrupt angling. The value of a single water vole was estimated by using a contingent valuation telephone survey giving a willingness to pay of approximately £10 per vole. The overall cost was obtained by multiplying this figure by the number of voles estimated to have been killed by mink (Williams et al. 2010). The other costs are estimated from the management expenditure specifically targeting the protection of heritage buildings or recreational enjoyment of waterways. Yet it is unclear to what extent management costs adequately capture the value of ecosystem services. Comparison of the management and ecosystem service costs reveal that costs on controlling non-native species underestimate the actual ecosystem service cost, often by one or more orders of magnitude (Table 21.1). Furthermore, the absence of any correlation between ecosystem service losses and management costs indicate that using the latter to assess the former is a flawed approach. It is noteworthy that the analysis of the costs of non-native species in Great Britain focus on losses rather than the benefits non-native species might deliver to ecosystem services. For example, the non-native rainbow trout, *Oncorhynchus mykiss*, generates more than £24 million from angling in Scotland alone (Radford et al. 2004), yet there are no estimates as to whether this species impacts negatively on other ecosystem services through predation or competition with native species (Williams et al. 2010). A final complication is that management costs may even be viewed as benefits, as in the Working for Water programme in South Africa where the costs of labour to remove non-native trees was seen as a social benefit because it provided employment for marginalised sectors of society (Bullock et al. 2011). Such a similar reasoning might be applied where non-native species removal is undertaken by volunteers who gain benefits through physical activity and improved social interaction as well as a stronger sense of community. If the benefits of management are counted when assessing ecosystem services, then other benefits derived from non-native species should be assessed when estimating overall costs.

21.2.4 Integrating Impacts on Ecosystem Services in Non-native Risk Assessment

Current risk assessment tools addressing impacts on ecosystem services do not attempt monetary evaluation but apply a scoring approach based on expert assessment using broad categories of loss. The European Food Safety Authority (EFSA 2014; Gilioli et al. 2014) uses five categories: Minimal (zero or negligible), Minor ($0 < M = 5$ %), Moderate ($5 < M = 20$ %), Major ($20 < M = 50$ %), and Massive ($M > 50$ %). These categories are then scored against six provisioning services (food; wood and fibre; genetic resources; biochemical, natural medicines, and pharmaceuticals; ornamental resources; and freshwater) and eight supporting/regulating services (air quality regulation; climate regulation; water regulation, cycling and purification; erosion regulation; soil formation and nutrient cycling; photosynthesis and primary production; pest and disease regulation; and pollination). However, impacts on cultural services are not included in these risk assessments (EFSA 2011). Although the aim of qualitatively assessing impacts across a wide range of ecosystem services is laudable, the reality is that for most non-native species the absence of data would mean little more than guesswork when attempting to assess risks.

Measures of the percentage loss in an ecosystem service require a knowledge of the total value impacted by non-native species. Yet translating the perceived percentage loss into monetary value is often difficult, as illustrated by the impact of three non-native species on forestry in Great Britain. Green spruce aphid feeding on spruce plantations results in a 3 % yield loss (£3.57M), whereas the great spruce bark beetle, *Dendroctonus micans*, causes an approximate yield loss of 0.25 % (£0.13M), and rabbits damage 5 % of seedling and saplings, which is estimated to reduce timber value by £62.02M (Williams et al. 2010). The key issue here is that non-native species impacts will vary in both quantity (e.g., yield) as well as quality (timber value) of the ecosystem service. In addition, such scoring schemes provide little opportunity to weigh the costs across different ecosystem services. For example, in terms of the function of an ecosystem or the benefits derived from it by humans, a 50 % reduction in erosion regulation may not be equivalent to a 50 % loss in pollination service, if erosion is a relatively insignificant aspect structuring the ecosystem but pollination is essential for the resident plant and insect communities. Thus, for each ecosystem service, a weight would need to be applied to enable integration of scores.

The level of detail required in a risk assessment on the impacts of a particular non-native species on ecosystem services depends on its expected outcome. If the tool is primarily to screen species as to whether there should be phytosanitary regulation to prevent intentional or unintentional introduction, then possibly a coarse qualitative system may suffice because the interest is in identifying the likelihood and degree of certainty required that the impact on one or more ecosystem services will not exceed a specified level. If, on the other hand, a tool is required to prioritise management among non-native species and invaded ecosystems, greater resolution and standardisation of scores will be required. Finally, if it is to be used in terms of quantifying the costs on non-native species to stimulate financial and legislative instruments to curb invasions, then monetary values derived from robust and repeatable methodologies will be needed.

21.3 Conflicts in the Contribution of Non-native Species to Ecosystem Services

The management of ecosystem services to optimise the human benefits derived from biodiversity often leads to conflicts in terms of what aspects should be prioritised (Bullock et al. 2011). For example, all ecosystem services are needed to a certain extent, which limits the scale at which optimizing of certain services can occur. Thus, provisioning services cannot be optimized everywhere because space for other services is also needed. In this regard, non-native species are not unusual in challenging an ecosystem service-based approach to biodiversity conservation (Vilà and Hulme 2017). However, an important difference is that non-native species are often agents of change and can be associated with both benefits and costs that each fall on different sectors of society (Deines et al. 2016).

Table 21.2 Summary of the main positive and negative impacts of tree of heaven *Ailanthus altissima* on ecosystem services, summarized from Sladonja et al. (2015)

	Positive impact	Negative impact
Provisioning		
	Medicinal	
	Agriculture pharmaceutical use	
	Honey production	
	Timber	
	Food for silkworms	
	Paper production	
	Essential oil source	
Regulating		
	Erosion control	Infrastructure damage
	Land reclamation	Allelochemical production
	Reforestation	
	Shelterbelts	
Cultural		
	Ornamental	Allergenic pollen
	Shade	Dermatitis
		Malodorous
Supporting		
	Primary production	Loss of biodiversity
	Carbon sequestration	Nutrient cycling
	Soil formation	

Not all non-native species provide ecosystem benefits. Most non-native species unintentionally introduced by humans are unwanted, often pathogens, pests, or weeds of crops. However, the majority of non-native species are introduced intentionally for use as crops, livestock, pets, game animals, or ornamental species and either are deliberately released into the wild or escape captivity (Hulme et al. 2008). Intentionally introduced species are thus often the source of conflict between different sectors of society because such species are perceived as having both benefits and costs. This is the case even for species that are widely regarded as among the worst non-native species in a region, such as tree of heaven, *Ailanthus altissima*,in Europe (Table 21.2). There are clear examples of these conflicts in terms of provisioning services (Gozlan 2017; Witt 2017) and cultural services (Kueffer and Kull 2017). The invasion of non-native conifers and ornamental plants into protected areas in New Zealand illustrates these two classes of conflict. For example, ornamental Russel lupins, *Lupinus polyphyllus*, outcompete native plant species, increase nitrogen input into aquatic systems, and reduce breeding habitat for endangered birds but have been deliberately sown by the public to beautify the landscape and are appreciated by visiting international tourists (Fig. 21.1).

The nature of conflicts arising from non-native species may take various forms, each potentially requiring different solutions. Five scenarios can be explored to illustrate these potential conflicts (Fig. 21.2). Compared to a reference non-invaded

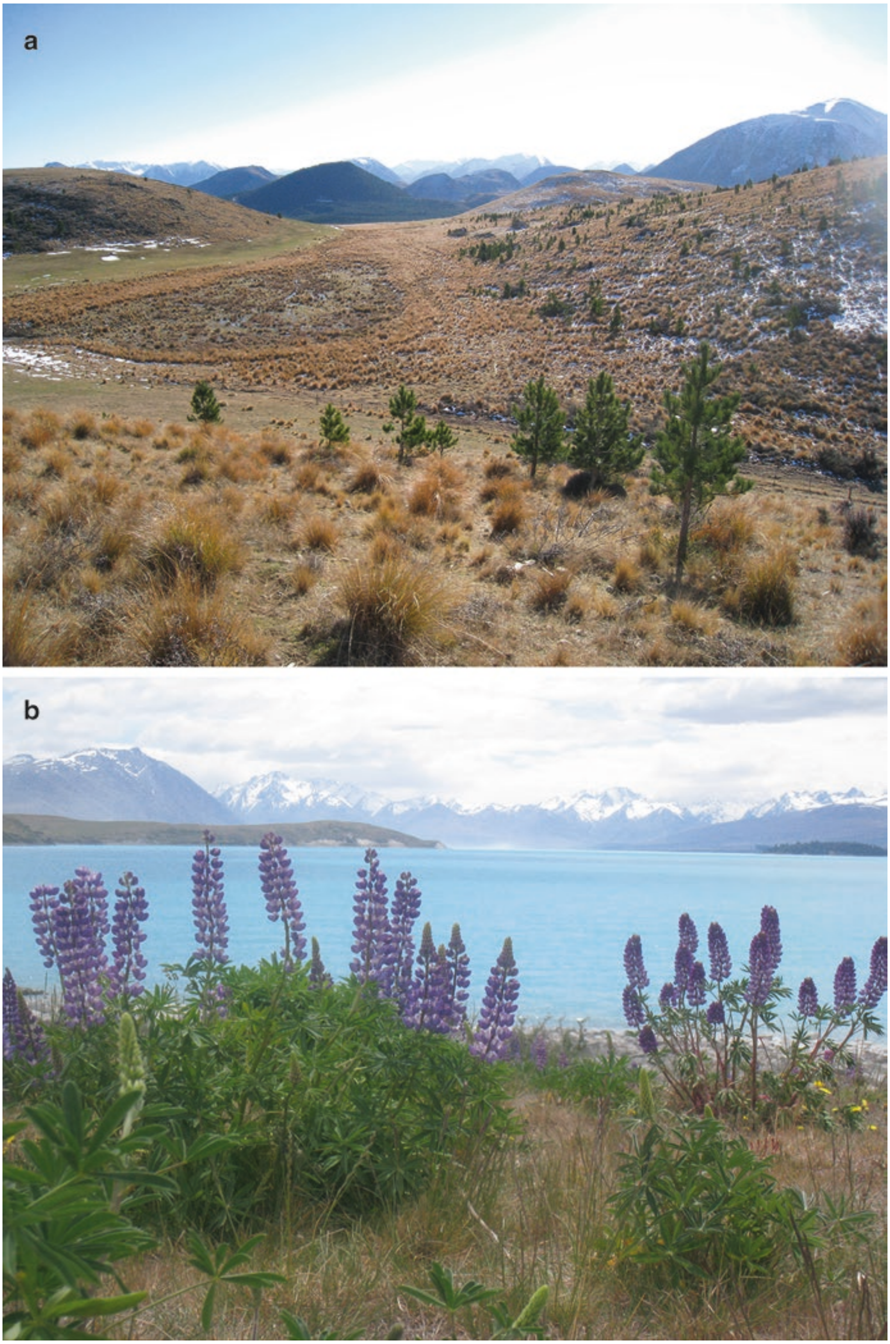

Fig. 21.1 (**a**) In New Zealand, non-native conifers have spread from plantations and colonised open grasslands with resultant changes in carbon sequestration, nutrient and water cycling, and the aesthetics of these open ecosystems. (**b**) Ornamental Russel lupins, *Lupinus polyphyllus*, outcompete native plant species, increase nitrogen input into aquatic systems, and reduce breeding habitat for endangered birds, but have been deliberately sown by members of the public to beautify the landscape and are appreciated by visiting international tourists (Photographs by Philip Hulme)

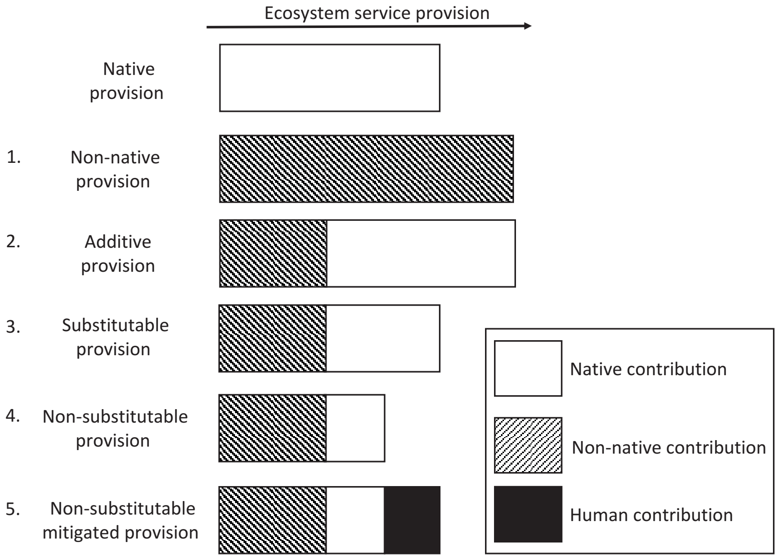

Fig. 21.2 Illustration of five different scenarios relating to the impact of non-native species on ecosystem service provision

native ecosystem, the replacement of all native species by one or more non-natives may increase the provision of a particular ecosystem service (scenario 1). This is a likely scenario for the invasion of grassland habitats by forestry species that shift the composition of native communities towards a non-native-dominated ecosystem that delivers significantly higher carbon sequestration, reduced soil erosion, and improved soil productivity. In most cases, the complete replacement of the native community does not occur and yet the incorporation of non-native species at the costs of natives improves overall ecosystem service (scenario 2), as in the case where non-native pasture grasses spread into indigenous grasslands, improving the value of the ecosystems for grazing livestock. These two scenarios illustrate situations where the conflicts of optimising ecosystem service provision will be most intense among stakeholders because there are clear economic benefits that can be obtained from the non-native species invasions into natural ecosystems. Such conflicts may be lessened if invasion by non-native species leads to a loss of native species but no net increase in ecosystem service provision since it would be hard for anyone to argue against the status quo (scenario 3). Nevertheless, under this scenario, the incentive to restore the ecosystem will be much less than in situations where invasions results in both a net loss of native species as well as ecosystem service provision, such as where a non-native weed reduces both the species richness as well as the palatability to livestock of grassland ecosystems (scenario 4). Where society places considerable value on the ecosystem service that is lost as a result on the invasion by non-native species and invests in mitigating such losses, such as in improving nutrient retention in invaded wetlands, there will be a stronger incentive to manage non-native species to improve ecosystem services (scenario 5).

Although these scenarios are purely illustrative, they highlight that a single solution to tackling conflicts is unlikely and that each situation requires a context-specific appraisal, requiring quantitative data on ecosystem service provision (King et al. 2015). The multidimensional nature of ecosystem services means that conflicts may be stronger for some services than for others (Vilà and Hulme 2017). Thus, ecosystem service approaches that only quantify the "most important" services may not be adequate for conflict resolution. Indeed, in some cases, conflict resolution may involve management rather than eradication of a particular non-native species if this species proves to be appreciated by certain stakeholders. Also, conflicts might prove particularly difficult to resolve if the main stakeholder deriving benefits from non-native species does not bear the cost of any negative impacts on ecosystem services, especially where the benefits and costs occur in different ecosystems (e.g. cropland versus native habitat), or between different economic sectors (e.g., industry versus ecotourism). Under these circumstances, before any introduction of a new crop, a polluter-pays principle might be adopted that involves insurance or environmental bonds to internalise the costs of non-native species (Driscoll et al. 2014).

21.4 Conclusions

As the international momentum increases to apply ecosystem service perspectives to a wide range of environmental and conservation-related issues, it is increasingly important that this approach can be applied to the prevention and management of harmful non-native species. However, at present the opportunity for such integration is limited by the lack of quantitative information on impacts on ecosystem services assessed at appropriate spatial and temporal scales to inform policy. Current environmental risk assessment frameworks have been extended to include socioeconomic impacts, but these have yet to be applied to the more complex issues arising from biological invasions wherein valuation of impacts on ecosystem services differs among stakeholders and sectors. Addressing the impacts on ecosystem services will require understanding of environmental conflicts and policy tools that can better capture impacts of commercially important non-native species.

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