Chapter 2. Trends and status of alien and invasive alien species[1]

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This chapter should be cited as: Seebens, H., Meyerson, L. A., Rahlao, S. J., Lenzner, B., Tricarico, E., Aleksanyan, A., Courchamp, F., Keskin, E., Saeedi, H., Tawake, A., and Pyšek, P.

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(2023). Chapter 2: Trends and status of alien and invasive alien species. In: Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Roy, H. E., Pauchard, A., Stoett, P. and Renard Truong, T. (eds.). IPBES secretariat, Bonn, Germany. https://doi.org/10.5281/zenodo.7430725

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Executive summary

1. At least 39,215 alien species and more than 37,000 established alien species have been recorded worldwide and occurrences of established alien species have been reported from all countries and all ecosystems globally (*established but incomplete*) {2.2.2}. Among these, 5,256 species have been classified as invasive according to the database underlying this chapter (*established but incomplete*) {2.2.2}. The distribution of established alien species shows marked hotspots of high species numbers, mostly located in North America, Europe, and Australasia, but also in individual African and Asian countries (*established but incomplete*) {2.2.2}. However, low data availability, particularly in Africa and Central Asia, suggests that many more unrecorded established alien species are extant but not reported due to a lack of monitoring and data integration (*established but incomplete*) {2.1.3, 2.1.4, 2.7}. Thus, the reported numbers of alien, established alien, and invasive alien species are likely severely underestimated (*well established*) {2.1.3., 2.1.4}.

2. The number of established alien species has risen at continuously accelerating rates for centuries, recently reaching the highest total number of established alien species and highest annual rate of new records (*established but incomplete*) {2.2.1}. The rise in established alien species numbers has had periods of uniform increases and marked accelerations (*well established*) {2.1, 2.2.1}. Before 1800, the introduction of alien species was largely driven by European colonialism, while recently introductions for ornamental purposes or associated with international transport have become more important pathways (*well established*) {2.1, 2.1.2, 2.3.1.2, 2.3.1.6, 2.4.2.2, 2.4.5.2, Box 2.5}. Marked accelerations of alien species introductions were observed circa 1800 and post-1950, currently reaching the highest value yet; 37 per cent of documented alien species introductions over the last two centuries have occurred since 1970 (*established but incomplete*) {2.1}. In addition to total numbers, the rate of increase of newly recorded alien species, which later became established, has also continuously risen with approximately 200 new alien species now recorded annually worldwide (*established but incomplete*) {2.2.1}.

3. In absolute values, the highest numbers of established alien species records have been reported for vascular plants, insects, fishes, fungi, and molluscs (*established but incomplete*) {2.2.2}. The distribution of established alien species worldwide is similar across taxonomic groups, with hotspots located in North America, Europe, and Australasia (*established but incomplete*) {2.2.2}. Vascular plants and mammals are the most widespread invasive alien species (*well established*) {2.2.2}. Temporal trends of records revealed three main patterns: For vascular plants, the number of records and the rate of increase rose distinctly from the nineteenth century to the present (*well established*) {2.3.2.1}, while for invertebrates, algae, and microorganisms, numbers and rates showed a marked increase particularly after 1950, likely due to increasing trade (*established but incomplete*) {2.3.1.6; 2.3.1.8, 2.3.1.9, 2.3.2.3, 2.3.3}. Mammals represent the only taxonomic group where the rate of new annual records has consistently declined since 1950, likely as a result of stricter regulations. However, while declining, the rate is still positive resulting in additional new alien mammal records each year (*established but incomplete*) {2.3.1.1}.

4. The total numbers of established alien species are similar in all IPBES regions except for Africa, ranging from 14,797 to 17,628 established alien species in the Americas, Europe and Central Asia, and Asia and the Pacific; total numbers are distinctly lower for Africa, which hosts a maximum of 6,484 established alien species (*established but incomplete*) {2.4.1, 2.4.2, 2.4.3, 2.4.4, 2.4.5}. The lower number of established alien species in Africa likely results from a combination of reduced introduction effort and lower data availability; therefore, the true number of alien and invasive alien species is expected to be markedly higher in Africa than currently reported (*established but incomplete*) {2.4.1}. Likewise, rates of increase were similar among the Americas,

Europe and Central Asia, and Asia and the Pacific, but lower for Africa where data are less complete (*established but incomplete*) {2.4.2, 2.4.3, 2.4.4, 2.4.5, 2.7}.

5. The majority of established alien species have been reported from terrestrial ecoregions (75 per cent), while distinctly fewer established alien species were recorded in freshwater and marine ecosystems (*established but incomplete*) {2.5.1, 2.5.2, 2.5.3, 2.5.4}. In part, this pattern reflects the natural distribution of species across ecosystems. However, aquatic habitats and marine systems in particular are less thoroughly sampled in comparison to terrestrial systems, suggesting that many more alien marine species have not been detected and recorded (*established but incomplete*) {2.5.2, 2.5.3, 2.5.4}.

6. The number of established alien species is expected to rise further with a predicted 36 per cent global increase by 2050, but with large variations by region and among groups of organisms; most existing established alien species are expected to expand their current ranges (*established but incomplete*) {2.6.1}. Annual rates of increase are predicted to rise further for invertebrates, such as insects and molluscs, likely as a consequence of anticipated increasing trade and transport, but to decline for mammals, probably due to efforts to prevent their introduction and spread (*established but incomplete*) {2.6.1}. However, models and scenarios to project biological invasion dynamics are scarce and underdeveloped, hindering a robust assessment of future dynamics (*well established*) {2.6.5}. Although some established alien species have reached their geographic range limits, most established alien species are likely to further expand their alien ranges in the near future (*established but incomplete*) {2.6.1}.

7. The number of established alien species is consistently lower on land managed by Indigenous Peoples (*established but incomplete*) {Box 2.6}. Indigenous Peoples' lands are often remote and host more natural habitats compared to other lands, but that has not protected them from alien species introductions. A total of 6,351 established alien species and 2,355 invasive alien species have been recorded worldwide on Indigenous Peoples' land (*established but incomplete*) {Box 2.6}. Hotspots of biological invasions on Indigenous lands with high numbers of established alien species are found on all inhabited continents but especially in Australasia, North America, and Europe (*established but incomplete*) {Box 2.6}, regions that have the highest established alien species numbers in general. Invasive alien species affect the livelihoods and good quality of life of Indigenous Peoples and local communities worldwide (*established but incomplete*) {Box 2.11}. However, most available studies on lands of Indigenous Peoples and local communities and on good quality of life focus on woody vascular plants, while much less information is available for the effects of other taxa, particularly microbes and insects (*established but incomplete*) {Boxes 2.6 and Box 2.11}.

8. Islands generally host high numbers of alien and invasive alien species (*well established*) {Box 2.5}. Compared to mainland areas, the number of established alien species on islands is often very high (*well established*) {Box 2.5}. For vascular plants, the numbers of established alien species exceed the total number of native species on many islands, doubling the plant species richness on those islands (*well established*) {Box 2.5}. Worldwide, widespread invasive alien species on islands include mammals such as *Rattus* spp. (rats), *Mus musculus* (house mouse), and *Felis catus* (cat), and plants such as *Leucaena leucocephala* (leucaena), *Lantana camara* (lantana), and *Ricinus communis* (castor bean) (*well established*) {Box 2.5}.

9. Research intensity and data availability documenting established alien species' occurrences have increased in recent decades, but information about alien species distributions remains incomplete, particularly for inconspicuous species such as invertebrates, microorganisms, and aquatic species (*well established*) {2.1.4, 2.2.2, 2.7}. Lists of established alien species occurrences are very likely incomplete in the vast majority of cases across in the world (*established but incomplete*) {2.1.3, 2.1.4}. There are, however, major critical gaps for many species groups in large

parts of Africa and Central Asia, for invertebrates and microorganisms, and for marine and freshwater species worldwide (*well established*) {2.2.2, 2.3.1.11, 2.3.2.5, 2.3.3.3, 2.4.2.5, 2.4.5.5, 2.5.1}. Gaps in recording alien species occurrences result in incomplete alien species lists and prevent a fully comprehensive assessment of the trends and status of invasive alien species across all taxa and habitats (*established but incomplete*) {2.2.2}. Further uncertainty arises from time lags that can span several decades from species introductions to their first detection (*well established*) {2.2.1, 2.2.3}, very likely making the documented numbers of established alien species a severe underestimate of the true extent of biological invasions (*well established*) {2.2.1, 2.2.2}. Importantly, incomplete data does not preclude drawing robust conclusions about alien and invasive alien species (*well established*) {2.7}. By taking data uncertainty into account, experts can provide a complete, credible, and transparent assessment that can be updated as more information becomes available (*well established*) {2.7}.

10. A global assessment of biological invasions that covers the trends and status of regions and species groups equally can be achieved by a major increase in efforts to monitor alien and invasive alien species and by standardizing protocols for handling and sharing data at a global scale (*established but incomplete*) {2.7}. Closing knowledge gaps in all regions and species groups and improving understanding of biotic and abiotic interactions that influence how species respond to environmental changes can be achieved through consistent, repeatable, and comparable studies of alien species occurrences that are deposited into publicly available repositories (*established but incomplete*) {2.7}. Additional applications of technology (e.g., remotely sensed data, environmental DNA) applied at large spatial scales can also provide comprehensive coverage of alien and invasive alien species (*established but incomplete*) {2.7}. Engagement by and with policymakers, citizen scientists, and Indigenous Peoples and local communities worldwide is critical to close data and knowledge gaps (*established but incomplete*) {2.7}.

2.1. Introduction

Assessing current and future dynamics of biological invasions requires data and knowledge on the geographic extent of invasive alien species, which can be used to identify hotspots of invasive alien species (**Glossary**). Further, a more comprehensive assessment depends on information about temporal trends (**Glossary**) to evaluate past and potential future species spread and detailed information on **alien** species, which while not yet classified as invasive in certain regions could become invasive in the future. To achieve a comprehensive global assessment of biological invasions, this chapter includes information on temporal trends and spatial distributions of both **alien** and **invasive alien species** (a subset of alien species).

Humans have introduced species to regions outside of their native ranges (**Glossary**) for millennia, and throughout, these introductions have undergone different periods of acceleration. As early as approximately 8000 B.C., neolithic people unintentionally distributed plant seeds when transporting crops (e.g., Di Castri, 1989). The first evidence of agricultural crops being traded over long distances comes from the Pharaohs of ancient Egypt approximately 3,000 to 1,500 years ago (Janick, 2007) and from Mesoamerica around the same period (Sanchéz, 1997). While early reports are scarce and inaccessible, evidence of increasingly frequent species exchanges has accumulated. The intensity of biotic exchange is often related to the extent and power of a particular empire, such as the Romans, Greeks, Aztecs, Polynesians, or the Han Dynasty. All introduced a variety of species throughout their reigns that continue to survive in their new locations (P. A. Cox & Banack, 1991; Di Castri, 1989; Ma et al., 2003; Sanchéz, 1997). As these empires expanded and the capacity of humans to travel long distances improved, there was a concomitant rise in the magnitude of alien species introductions.

The establishment of sea routes between Europe, the Americas, Africa, and Asia in the fifteenth century marked the onset of a truly global trade network that facilitated a continuously growing rise in alien species introductions (**Figure 2.1**; Di Castri, 1989) but the extent of increase varied considerably between taxonomic groups and geographic regions. Nonetheless, there has been a marked intensification of alien species exchanges across all taxonomic groups and regions in the last 200 years; the nineteenth century and post-1950s eras experienced especially high increases of new species introductions, i.e., 37 per cent of all documented established alien species introductions have occurred since 1970 (Bonnamour et al., 2021; Seebens, Blackburn, et al., 2017). Given the incomplete and inconsistent records of documented historic introductions, it is likely that past introduction rates were even higher (Seebens, Blackburn, et al., 2017).

While many species have been unintentionally introduced, other introductions in the pre-historic, historic, and modern eras have been intentional, occurring for purposes including food, horticulture, sport hunting and fishing, the fur trade, the pet trade, and for nature's contributions to people such as erosion control and biological control (**Glossary**; e.g., Eviner et al., 2012; Genovesi et al., 2009; Luken & Thieret, 1997; R. M. Pringle, 2005; Reichard & White, 2001; Simberloff, 2012). The introduction pathways (**Glossary**) and the taxa introduced have varied over time (**Table 2.1**; **Figure 2.2**).

The introduction of alien species is coupled with human activities and it is therefore unsurprising that invasion trends and human socio-economic activities are closely linked (Hulme, 2009; Levine & D'Antonio, 2003; X. Liu et al., 2019; Meyerson & Mooney, 2007; Pyšek, Jarosik, et al., 2010). Different drivers may affect invasion dynamics and become important during different stages of the biological invasion process (**Glossary**), such as the introduction and establishment stages. For instance, global trade and transport are well-known major drivers promoting the intentional or unintentional introduction of alien species (**Chapter 3**, **section 3.2.3**; and Hulme, 2009). Tourism is another important driver (**Chapter 3**, **section 3.2.3.4**), particularly on remote islands (Toral-Granda

et al., 2017). But interactions between introduction pathways and invasion stages also vary by taxonomic group (e.g., Bernery et al., 2022). Anthropogenic disturbances such as habitat (**Glossary**) destruction (e.g., deforestation), degradation (e.g., eutrophication) and fragmentation, and climate change are strongly associated with increasing habitat vulnerability to invasions (Hierro et al., 2006; Hulme, 2017; Pauchard & Alaback, 2004; J.-Z. Wan et al., 2019). Thus, once introduced, alien species are more likely to establish in areas with high degrees of land use change, high human population density, and high gross domestic product (GDP) (Pyšek, Jarosik, et al., 2010). All of these drivers have distinctly increased in the last decades (**Figure 2.1**; **Chapter 3**, **section 3.1.1**), paving the way for rising numbers of invasive alien species, and the establishment of alien species more generally.

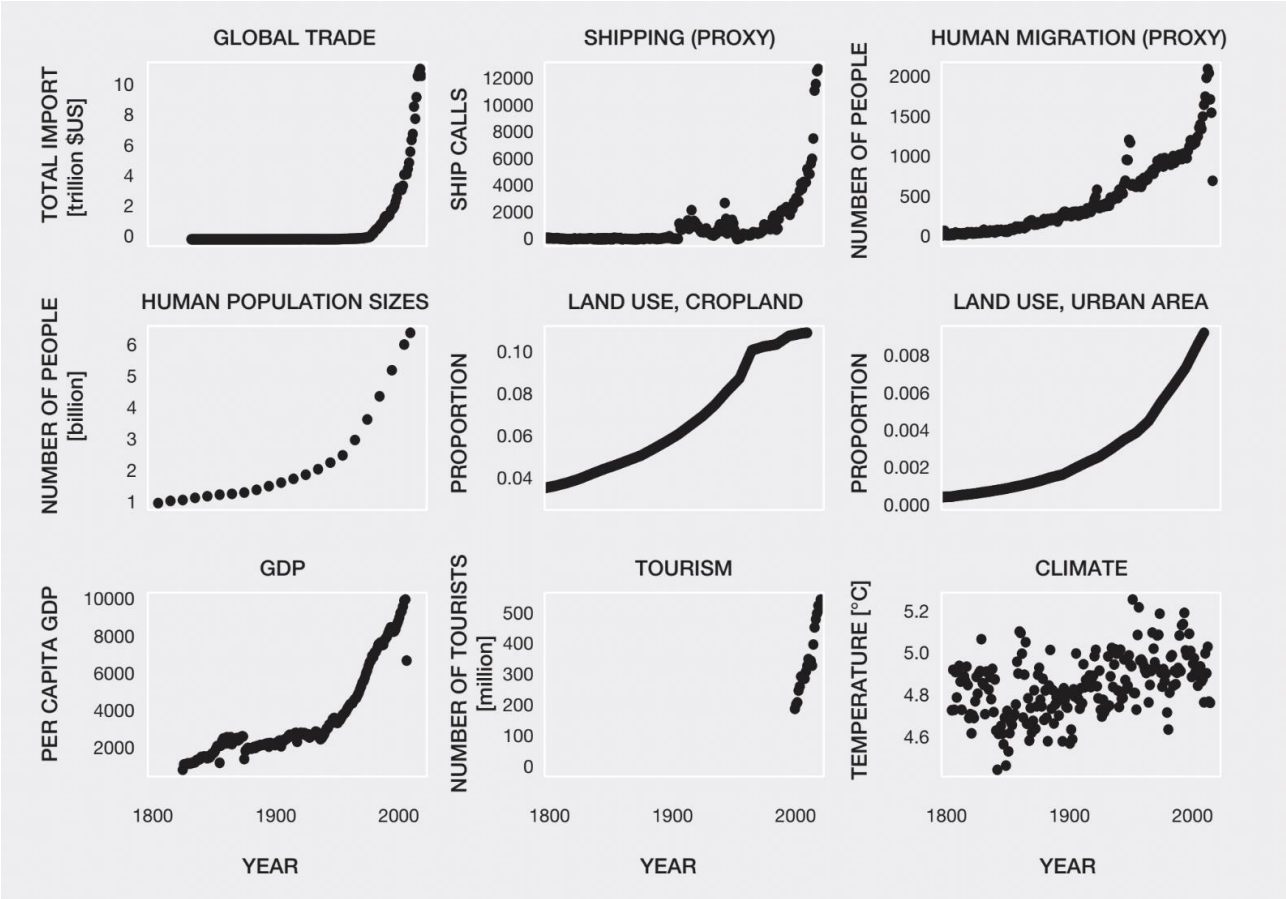

Figure 2.1. Trends in drivers of change in nature and correlates of biological invasions. Panels show temporal trends of a selection of main drivers and correlates of biological invasions averaged globally. For "shipping" and "human migration" only proxy variables are shown due to the lack of more comprehensive data covering the full time period. Although these proxy variables represent only subsets of the full dynamics, they well indicate the overall temporal patterns of change. A data management report for this figure is available at https://doi.org/10.5281/zenodo.7615582

2.1.1. Previous alien and invasive alien species assessments

Multiple recent regional and global scale assessments have highlighted biological invasions as having a significant influence on nature (**Glossary**), nature's contributions to people, good quality of life and on Indigenous Peoples and local communities (**Glossary**; IPBES, 2018a, 2018b, 2018c, 2019a). In general, these assessments have noted that while progress has been made in identifying pathways of alien species introductions and in invasive alien species eradication and management (**Glossary**; Secretariat of the CBD, 2020), successful prevention of biological invasions (**Glossary**) remains limited, in part due to ineffective border controls in some countries (Secretariat of the CBD, 2014). Global and regional assessment reports show that biological invasions are an

increasing worldwide threat (Early et al., 2016; Osipova et al., 2017; WWF, 2018) exerting pressure on native biodiversity in concert with other global phenomena (IPBES, 2016; Secretariat of the CBD, 2020) resulting in consequences such as biotic homogenization and the extinction of native species (**Glossary**; Millennium Ecosystem Assessment, 2005). However, both positive and negative impacts (**Glossary**) associated with alien species have been documented (IPBES, 2016; Roué et al., 2017). Nonetheless, large swathes of several regions remain understudied and report relatively little information regarding invasive alien species (IPBES, 2018b). In Europe, Central Asia, and in the Americas, biological invasions are severe due to extensive trade and transportation networks that are pathways for alien species introductions (IPBES, 2018b, 2018c) with more complete documentation in Europe and North America. In Central Asia, South America and mesoamerica, and in Africa, biological invasions tend to be less well-documented and few sources on the biogeographic details of invasive alien species trends are available across these regions (IPBES, 2018a, 2018b, 2018c). Further, invasive alien species are identified by Indigenous Peoples and local communities as one of the major drivers of change in nature as, for example, these species encroach on grazing lands and threaten agricultural systems (Forest Peoples Programme et al., 2020; Roué et al., 2017). Many invasive alien species do not have any cultural or economic value for Indigenous Peoples and local communities and some groups lack strategies to deal with biological invasions (Roué et al., 2017).

2.1.2. Pathways of alien species introductions

Following standard frameworks (CBD, 2014; Hulme et al., 2008), pathways describe the mechanisms that result in the introduction of alien species. Pathways usually focus on movements until a species reaches the border of an administrative unit, such as a country, although they are not restricted to this definition. Pathways are distinct from routes of introduction; pathways describe how and by what means a species has entered the new region; route of introduction refers to a geographic route between two locations. Pathways have been categorized into six major classes (release, escape, contaminant, stowaway, corridor, and unaided) and several sub-classes. Major classes of pathways are provided by the Convention on Biological Diversity (CBD; CBD, 2014; **Table 2.1**; **Chapter 1**, **Box 1.6**).

Table 2.1. Definition of major pathway classes

Definitions are published by the CBD (2014).

Pathway class	Definition
Release in nature	The intentional introduction of live alien organisms for the purpose of human use in the natural environment. Examples include biological control, erosion control, releases for fishing or hunting in the wild, landscape "improvement" and introductions of threatened organisms for conservation or religious purposes.
Escape from confinement	The movement of (potentially) invasive alien species from confinement (e.g., zoos, aquaria, botanic gardens, agriculture, horticulture, forestry, aquaculture and mariculture facilities, scientific research or breeding programmes, or escaped pets) into the natural environment. Through this pathway, organisms were purposefully imported or otherwise transported to confined conditions, but subsequently unintentionally escaped confinement.
Transport–Contaminant	The unintentional movement of live organisms as contaminants of a commodity that is intentionally transferred through international trade, development assistance, or emergency relief. This includes pests and diseases of food, seeds, timber, and other products of agriculture, forestry, and fisheries, as well as contaminants of other products.
Transport–Stowaway	The moving of live organisms attached to transporting vessels and associated equipment and media. The physical means of transport-stowaway include various conveyances, ballast water and sediments, biofouling of ships, boats, offshore oil and

	gas platforms and other water vessels, dredging, angling or fishing equipment, civil aviation, sea and air containers.
Corridor	The movement of alien organisms into a new region following the construction of transport infrastructure without which spread would not have occurred. Such trans-biogeographical corridors include international canals (connecting river catchments and seas) and transboundary tunnels linking mountain valleys or oceanic islands.
Unaided	The secondary natural dispersal of invasive alien species that have been introduced by means of any of the foregoing pathways.

Alien species have been introduced through a variety of pathways that have varied in importance over time and among species groups (**Figure 2.2**; CBD, 2014; Faulkner et al., 2016; Hulme et al., 2008; Pyšek et al., 2011). Intentional introduction pathways, such as release and escape, have played a major role for plant and vertebrate introductions, while unintentional introduction pathways, such as contaminant and stowaway, are highly relevant for introduced invertebrates, algae, and fungi (Saul et al., 2017). In addition to variations among species groups, the relative importance of pathways for introducing alien species and the absolute number of alien species introduced through certain pathways has changed over time depending on the number of propagules being transported (van Kleunen et al., 2018). Overall, the absolute number of established alien species has increased across nearly all pathways with particularly steep increases beginning circa 1800 and continuing until the present (**Figure 2.2**). The main pathway recorded for most species was escape from confinement, followed by contaminant and stowaway, release in nature, and corridors. The relative importance of the escape pathway has declined slightly in recent decades, while the contaminant and stowaway pathways have increased in importance, possibly reflecting higher numbers of introductions through global trade and transport (Hulme, 2009). For detailed pathway classifications, seed contamination was the only pathway with declining absolute numbers, and particularly strong increases were observed for pet species and stowaways (**Figure 2.2**). Overall, introductions for ornamental purposes remained highest in absolute numbers over the last 200 years. However, most (82 per cent of all available records in the pathway data set by Saul et al. (2017)) information on pathways is available for plants and vertebrates, while information on introduction pathways is often lacking for other taxa. Therefore, the patterns and trends in pathway dynamics described above are likely biased towards pathways associated with plant and vertebrate introductions.

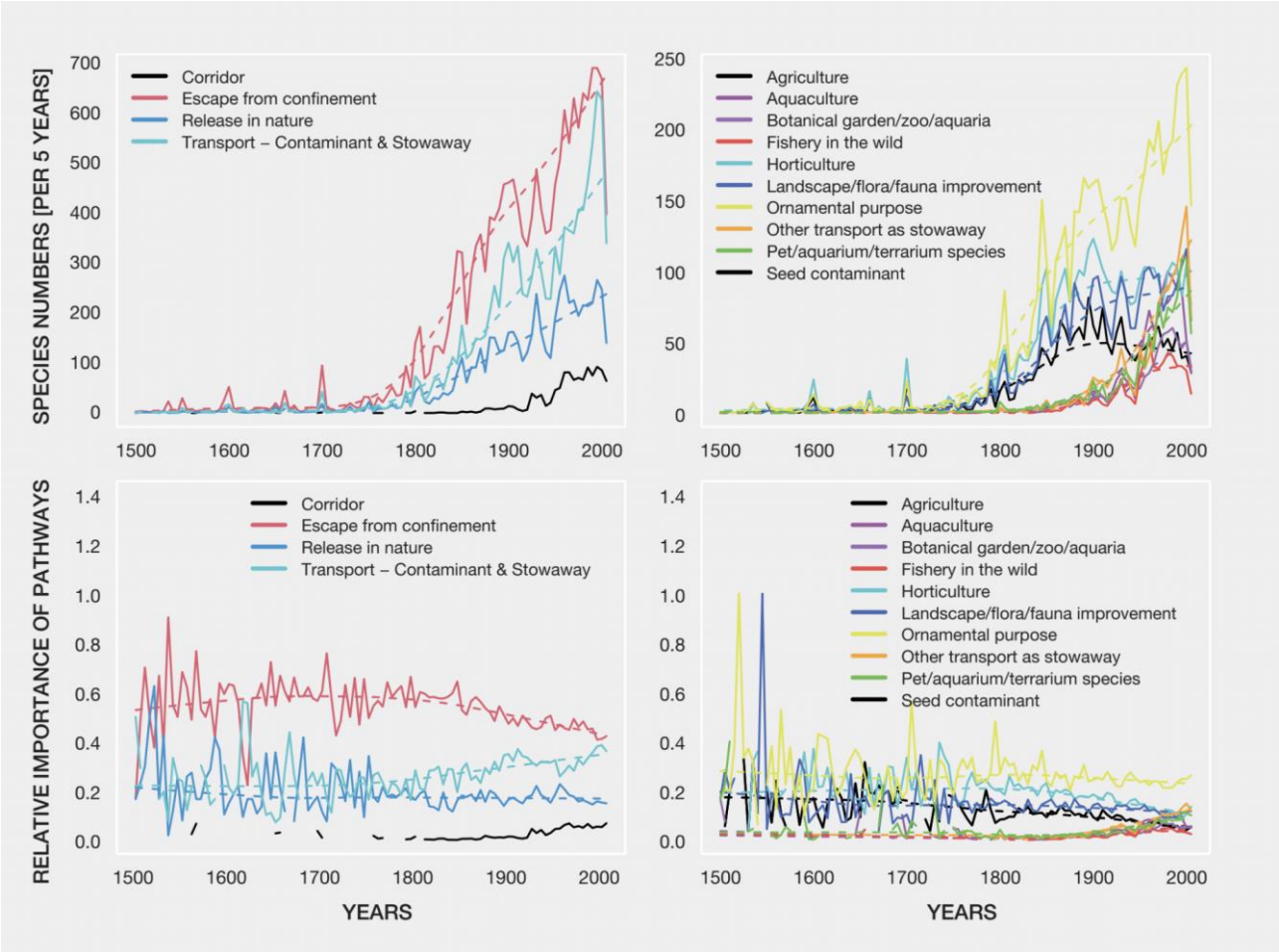

Figure 2.2. Introductions of established alien species by pathway over time. The figure shows global absolute numbers (top) and relative importance (bottom) of established alien species introductions by pathway since 1500. Smoothed trends are indicated by dashed lines. Sudden drops at the end of the time series likely reflect a lack of recent records. Only the top ten pathway sub-categories are shown. A data management report for this figure is available at https://doi.org/10.5281/zenodo.7615582

2.1.3. Chapter structure and content

Chapter 2 presents an overview of the current knowledge on the trends and status of alien species in general and invasive alien species. The logic underlying this chapter, the definitions of trends and status, and how the terms are used are presented in **Box 2.1**. Throughout the chapter, three distinct categories for species introduced to regions outside of their native ranges have been used: alien species, established alien species, and invasive alien species (**Chapter 1**, **Figure 1.1**, **Glossary**). These three status categories have been included because studies and databases vary in their definitions and details for these terms, some studies address only alien species without further specification, others focus on established alien species, while others distinguish among alien, established alien, and invasive alien species. It is critical to distinguish the status categories of species along the process of biological invasions for two main reasons, that is, because each term has a distinct meaning in invasion science and because the introduction dynamics, species distributions, and factors driving invasion patterns vary by taxa (Hejda et al., 2009). The ability to clearly delimit invasive alien species from established alien species is impacted by a lack of standardized definitions systematically applied across studies and databases. Moreover, the status of a species introduced outside of its native range can change at any given time, further complicating

assessments. Consequently, it remains difficult to consistently and comprehensively collate information on invasive alien species trends and status only; thus, alien and established alien species are also considered. This chapter does include one figure depicting temporal trends of invasive alien species numbers (**Figure 2.4***,* in **section 2.2.1**) and multiple tables of the most widespread (**Glossary**) invasive alien species as provided by the Global Register of Introduced and Invasive Species (GRIIS; Pagad et al., 2022). However, most available information and data are for established alien species. When known, the specific invasion status is therefore indicated throughout the chapter.

Box 2.1. Rationale of the chapter

Chapter 2 reports on past and future temporal trends in alien species (including established and invasive alien species where possible) numbers, their current and future status, and data and knowledge gaps for taxonomic groups, Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) regions, and units of analysis (**Chapter 1***,* **sections 1.6.4** and **1.6.5**). Temporal trends are long-term directional changes over long time periods (i.e., decades to centuries) in numbers of species, populations, or individuals introduced or in the spatial extent of colonization. Trends are presented as numbers of species (species richness) and rates of accumulation over time (i.e., numbers of newly recorded established alien species per unit time). Status is the current established alien species number and distributions in a certain area such as IPBES regions (**section** Error! Reference source not found.) or units of analysis (**section** Error! Reference source not found.) – and is indicated by established alien species number per spatial unit (global, regional, and biogeographic). Data and knowledge gaps describe missing or unavailable information or data for species or taxonomic species concepts, IPBES regions, or units of analysis.

Guiding questions:

What is the status of alien species globally, regionally, by taxon and by unit of analysis?
What are the trends for established alien species globally, regionally, by taxon, and by unit of analysis?
What are the data and knowledge gaps for alien species-related data and how do they vary globally, regionally, by taxon and by unit of analysis?
What are the eco-evolutionary dynamics of biological invasions?
What are the methodological limitations and uncertainties in future dynamics in invasive alien species?

Key words: alien species, established alien species, invasive alien species, distribution, status, trends, data gaps

The structure of the chapter is depicted in **Figure 2.3**. This chapter reports on trends, status, and gaps consistently across all major sections. The major sections represent first a general introduction (**section 2.1**) and an overview of the global dynamics (**section 2.2**) followed by trends, status, and gaps by taxonomic group (**section 2.3**), IPBES regions and subregions (**section** Error! Reference source not found.), IPBES units of analysis (**section** Error! Reference source not found.), and future projections (**section 2.6**). While this structure creates some redundancies, it provides comprehensive and focused information for readers interested in a particular group, system, or region. In addition, particular emphasis was given to selected topics of overall importance in individual boxes. Throughout the chapter the term "species" is used for clarity, though it should be noted that individual populations of a species, not the entire species, are invasive. Where appropriate, the distinction has been made between major species groups, namely mammals, birds, fishes, reptiles, amphibians, insects, spiders, crustaceans, molluscs, other invertebrates, vascular plants, aquatic vascular plants, algae, bryophytes, fungi, Chromista, bacteria, and viruses.

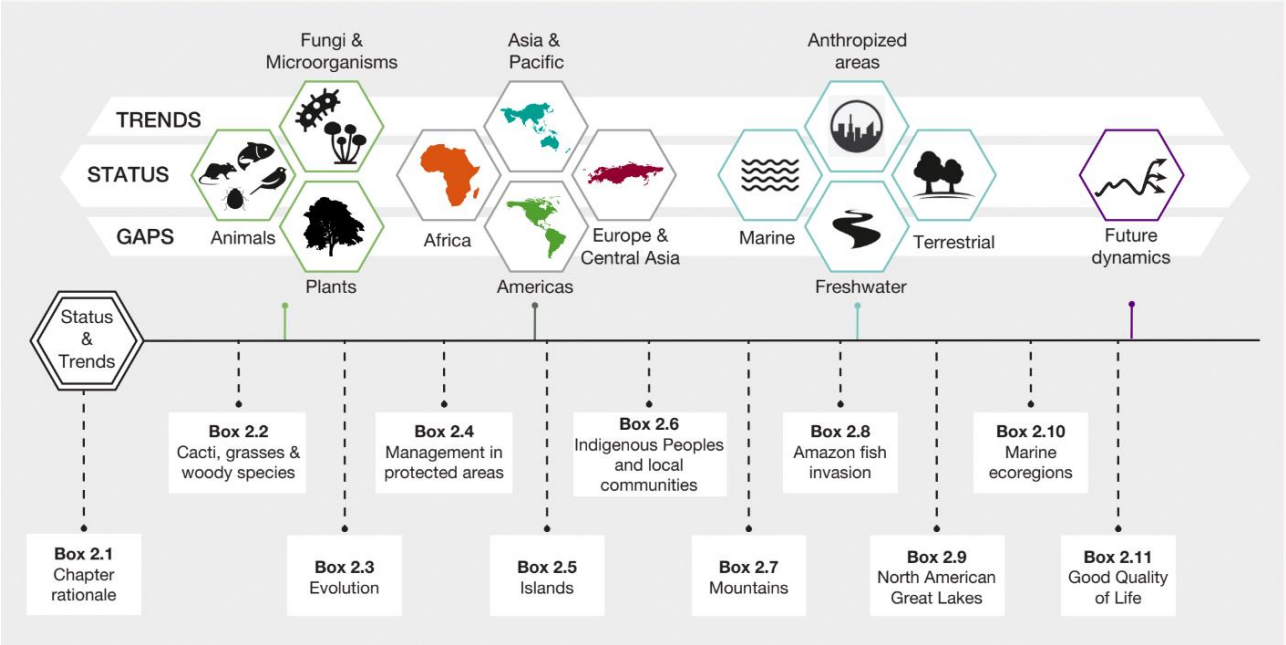

Figure 2.3. Overview of chapter structure. Chapter 2 reports on temporal trends, the status of the current distributions of alien and invasive alien species, and the gaps in knowledge for taxonomic groups, IPBES regions, units of analysis, and future dynamics. Case studies and in-depth presentations are provided in boxes throughout the chapter.

The trends and status of alien species as presented here are based on a comprehensive review of the existing literature and databases, supplemented by knowledge from experts from all around the world and from multiple biological disciplines. The authors strove to provide a globally and taxonomically balanced and comprehensive assessment of the trends and status of alien, established alien, and invasive alien species based on available knowledge and data. However, the information residing in alien species records occurrences is scattered and patchy. A large number of records for alien species occurrences are missing for multiple reasons such as data not being publicly available, delays entering records into available databases, lack of such databases at all, or few or no monitoring activities (**Glossary**), which is particularly problematic for certain taxa such as microorganisms and sub-regions such as Central Africa. Consequently, the numbers presented in figures and tables inevitably underestimate the true numbers of alien species occurrences. However, incomplete data does not imply that inferred conclusions are flawed; instead, it means that conclusions should be drawn carefully while considering the availability and potential biases of information. In this assessment of trends and status of biological invasions, the uncertainty due to incomplete data to provide robust conclusions that are scientifically supported by currently available evidence has been included.

2.1.4. Generation of data underlying figures and tables in this chapter

Due to the use of inconsistent terminology and data processing steps, a direct comparison of individual studies of alien species occurrences is often difficult. Comprehensive global databases that allow direct comparisons of numbers across taxonomic groups and regions exist for a few well-investigated species groups. These global databases provide comprehensive information at least for individual species groups and form the basis for a database generated for this chapter.[2] All numbers presented in the tables and figures in this chapter are based on this single database compiled specifically for this chapter if not stated otherwise. Consequently, the textual descriptions of the chapter provide a more comprehensive assessment of the existing literature for the respective

geographic unit or taxonomic group, while the figures and tables provide a basis for comparison across regions and taxa, which is inevitable based on a reduced number of records. The generation of the chapter database is described in detail below, and also provided in the data management report for this chapter. [2]

Generation of a database of regional checklists of alien species

The chapter database of alien species occurrences that provides the basis for figures and tables in this chapter[2] was established by integrating major global databases of alien species occurrences. These databases were selected because they are global, represent the most comprehensive databases in their field, and are published and freely accessible. Altogether, seven databases fulfilled these criteria (**Table 2.2**): five databases with a focus on individual taxonomic groups, and two cross-taxa databases, one of which contains years of first records of alien species. The development of these databases is based on more than 4,000 individual sources of information including scientific publications, reports, and regional databases. That is, although only seven databases are included, the total number of considered publications and data sources is considerably larger. Nonetheless, it is likely that even for the species groups and content included in the databases, not all available reports and studies were considered, and records are missing for a variety of reasons. As a consequence, the numbers of species reported in figures and tables of this chapter are likely higher.

Table 2.2. List of databases of alien and invasive alien species considered as a basis for figures and tables in this chapter

Database	Content used here	Citation and source
Global Naturalized Alien Flora (GloNAF)	Regional records of alien vascular plants	van Kleunen et al., 2019 https://idata.idiv.de/DDM/Data/ShowData/257
Global Avian Invasions Atlas (GAVIA)	Regional records of alien birds	E. E. Dyer, Redding, et al., 2017 https://doi.org/10.1038/sdata.2017.41
Distribution of Alien Mammals (DAMA)	Regional records of alien mammals	Biancolini et al., 2021 https://doi.org/10.6084/m9.figshare.13014368
Alien amphibians and reptiles	Regional records of alien amphibians and reptiles	Capinha et al., 2017 https://doi.org/10.1111/ddi.12617
MacroFungi	Regional records of alien macro fungi	Monteiro et al., 2020 https://doi.org/10.15468/2qky1q
Alien Species First Records (FirstRecords)	First records of alien species in regions across taxonomic groups	Seebens, Blackburn, et al., 2017 https://doi.org/10.5281/zenodo.4632335
GRIIS	Regional records of alien and invasive alien species across taxonomic groups	Pagad et al., 2022 https://doi.org/10.5281/zenodo.6348164

The seven global databases used as the basis for all figures and tables in this chapter differ in their spatial resolutions, terminologies, and taxonomies, impeding the direct integration of databases.[2] Assessment experts have therefore applied a workflow (i.e., a series of data transformation steps implemented in open-source computer scripts) to first standardize the spatial resolutions, terminologies, taxonomies, and the representation of years of first record. Synonyms were resolved according to the backbone taxonomy of the Global Biodiversity Information Facility (GBIF).

[2] The full workflow, including detailed descriptions and manuals, has been published (Seebens, 2021; Seebens et al., 2020). Version 1.3.9 of the workflow (https://doi.org/10.5281/zenodo.5562840) has been applied to produce the final database version 2.4.1, which is used in this chapter (https://doi.org/10.5281/zenodo.5562892). The data management report is also available at https://doi.org/10.5281/zenodo.7615582

Subsequently, the databases were combined, duplicated entries were removed, and conflicting entries, such as deviating first records, were resolved where possible. Conflicting entries that could not be resolved automatically, such as deviating invasion status, were kept as duplicated entries in the chapter database.[2] New workflows were developed to enable the identification of the biogeographical status of occurrence records using probabilistic frameworks (e.g., Arlé et al., 2021).

The integration of the seven global databases as described above resulted in the largest single database of alien species distributions currently available, containing 175,980 records of 39,215 alien taxa from 264 locations worldwide. The term "location" mostly refers to countries, but the database also contains information about sub-national units such as islands or federal states in some cases. The database also includes populations with unconfirmed or "casual" (**Glossary**) status. Records of casual species are not reported in this chapter and therefore excluding casual alien species resulted in 37,591 established alien species and 5,260 invasive alien species as classified by the database GRIIS.

The databases underlying the chapter database differ in their terminology describing biological invasion status (i.e., introduced, established, invasive) of a population (Groom et al., 2019). However, invasion status is often difficult to determine due to the lack of protocols for a standardized determination. Some databases, such as GloNAF, have a more rigorous and conservative approach to classifying established alien species, while other databases such as GRIIS included more species in this category. Consequently, the total numbers of established alien species vary among databases. Comprehensive global databases exist for mammals, birds, and vascular plants. These underwent a thorough assessment of invasion status and thus usually report lower numbers relative to cross-taxonomic databases such as the GRIIS or FirstRecords. To account for this variation in this assessment, total numbers of established alien species were provided as ranges for these taxonomic groups to emphasize the variation that exists in the published material. However, the spatial variations of the taxonomic databases are highly correlated with the variation in the GRIIS: The Pearson correlation coefficients, r, of total established alien species per region between GRIIS and GloNAF (r=0.92), Global Avian Invasions Atlas (GAVIA) (r=0.76) and Distribution of Alien Mammals (DAMA) database (r=0.82) were all high and significant. Thus, the spatial and temporal patterns as shown in this chapter do not distinctly differ among databases except in the overall levels of species numbers. This chapter therefore shows the total numbers of established alien species, including all databases in maps and time series, and provides ranges in tables of established alien species numbers.

Generation of a database of local occurrence records

The database used in this chapter provides information on alien species occurrences in so-called checklists representing lists of species for countries, large islands or other sub-national regions. This is inconvenient when it comes to the analysis of the distribution of alien species at other delineations such as units of analysis or marine ecoregions. To obtain information about alien species occurrences at different levels of spatial organization and scale, a freely available workflow to downscale regional checklists of alien species occurrences was applied (Seebens & Kaplan, 2022b). Using this workflow, coordinates of species occurrences as reported in the chapter database were obtained from GBIF and the Ocean Biodiversity Information System (OBIS). For each species in the chapter database, coordinates of records (marine or terrestrial) were obtained from the aforementioned online platforms and identified as representing alien populations based on the chapter database. Various steps of data cleaning and testing were included to avoid false entries. In this way, more than 35 million records of alien populations of 17,424 established alien species with coordinate-based records were gathered. These point-wise occurrence records were then aggregated to obtain total established alien species numbers per terrestrial region, marine ecoregion (see next paragraph for details, see also **Chapter 1, section 1.6.4** for a description of IPBES regions and sub-

regions used in the IPBES invasive alien species assessment), and land managed by Indigenous Peoples (**Box 2.6** in **section 2.4.1**). The full database of coordinates is open access (Seebens & Kaplan, 2022a), and includes a manual for data generation and digital object identifiers for GBIF requests to ensure reproducibility and transparency.

Marine records

Comprehensive information about the global occurrence of marine alien species was largely lacking when work on this chapter was initiated. Since then, two important developments have taken place, namely the publication of a worldwide study on marine alien species distributions (Bailey et al., 2020) and the publication of the World Register of Introduced Marine Species (WRiMS; M. J. Costello et al., 2021). In both cases, records of marine alien species have been validated by experts in the field. A total number of 1,442 marine alien species were recorded by Bailey et al. (2020), while 2,714 species were reported by M. J. Costello et al. (2021). Both are likely underestimates of the true extent of marine alien species. Due to the lack of more detailed data and/or available expertise to check individual records and regions, the studies cover either only approximately half of the world's marine ecoregions or provide information on comparatively large spatial units rendering a comparison of marine ecoregions difficult. To provide an alternative way of gathering information, this assessment used the database of local occurrence records of established alien species as described in the previous paragraph, which is based on regional checklists of established alien species and records from GBIF and Ocean Biodiversity Information System (OBIS) as described in the published workflow (Seebens & Kaplan, 2022b). The coordinate-based records were then assigned to the marine ecoregion as presented by Spalding et al. (2007). The spatial representation is still biased towards well-investigated regions and records are not cross-checked by experts, but the generated data do provide an overview across nearly all marine ecoregions worldwide. To consider the published data validated by experts, the information provided in Bailey et al. (2020) has been used where possible and filled in missing regional information by the aforementioned data generation methods.

Quantification of data gaps

The lack of information on alien and invasive alien species occurrences means that regional lists (i.e., checklists) of established alien species are often incomplete, producing data gaps. The degree of incompleteness varies by taxonomic group, region, and time period (Pyšek et al., 2008). To assess the influence of data gaps on the trends and status presented in this chapter, this assessment attempted to quantify the degree of incompleteness. As little research has been done previously to assess incompleteness, three different indicators of data gaps were tested:

1. The number of studies available per region in the chapter database was used as a proxy measure for research intensity and should negatively relate to data gaps.

1. To measure data gaps across taxonomic groups, the number of widespread phyla for which no information was available for a particular region was counted. A widespread phylum is defined as one with more than 500 records in the chapter database. Seven phyla were determined to be widespread: Ascomycota, Annelida, Basidiomycota, Mollusca, Chordata, Arthropoda, and Tracheophyta. Different cut-off values (other than 500 records) for selecting taxonomic groups were tested but did not change the overall patterns. The number of these phyla with less than five records per region was then counted. By applying this approach, experts assumed that at least five established alien species per selected phylum (i.e., at least five species of Tracheophyta per region, five established alien species of Arthropoda, etc.) should be found in each region as defined in the chapter database. This is likely true, particularly for large regions, but might be critical for very small regions and small islands. Different versions of this indicator were tested using different cut-off values (e.g., at least one, three, or ten records) but all versions

revealed similar spatial patterns of research intensity and data gaps (**Figure 2.5** for a spatial representation of indicators 1 and 2).

2. A third indicator was used to describe spatial variation of data gaps for individual taxonomic groups by comparing the number of available first records of established alien species for a region with the total number of species recorded for the same region. This analysis provided information on the proportion of available first records per region and can be used to assess the robustness of temporal trends and provide indications about the general availability of information for the respective taxonomic group. As the biases known for first records largely reflect data and knowledge gaps in general, the proportion of available temporal information is used as a proxy for data completeness.

Although none of these indicators are ideal, they can be considered for context when interpretating the trends and status of biological invasions.

2.2. Global trends and status of alien and invasive alien species

This section describes an assessment of the temporal trends and status of the distribution of alien and invasive alien species globally for all taxonomic groups combined.

2.2.1. Trends

Overall, studies on the introduction of alien species over time have reported a continuous global increase in the number of established alien species consistent across taxonomic groups, particularly since the early nineteenth century (Aukema et al., 2010; C. Chen et al., 2017; E. E. Dyer, Cassey, et al., 2017; S. Henderson et al., 2006; Peck et al., 1998; Pyšek et al., 2012; Roy, Preston, et al., 2014; Sandvik, Dolmen, et al., 2019; Sax & Gaines, 2008; Verloove, 2006; Wilson et al., 2007). Indeed, there is no study reporting a decline in established alien species numbers except for a few islands where eradication programmes or stringent biosecurity (**Glossary**) measures have been applied (Simberloff et al., 2013). Distinct increases in established alien species numbers are often reported post-1950 (Huang et al., 2011; Peck et al., 1998; Pyšek et al., 2012; Sandvik, Hilmo, et al., 2019), while a few other reports indicate earlier acceleration in the nineteenth century (mostly for vascular plants; C. Chen et al., 2017; S. Henderson et al., 2006; Seebens, Blackburn, et al., 2017; Wilson et al., 2007) or continuous increases without periods of acceleration over 200 years (mostly for insects; Aukema et al., 2010; Nahrung & Carnegie, 2020) and birds (Blackburn et al., 2015). In addition to the rise in cumulative established alien species numbers, many studies also report rising rates of increase over time (Blackburn et al., 2015; Seebens, Blackburn, et al., 2017). Recently, the highest global emergence rates of new established alien species were reported with approximately 200 new alien species, which later became established, recorded annually (Seebens, Blackburn, et al., 2017). Declining rates of new records of terrestrial alien species were observed only for vascular plants in North America (Seebens, Blackburn, et al., 2017), insects in Australia (Nahrung & Carnegie, 2020) and mammals worldwide (Seebens, Blackburn, et al., 2017). As shown in the GRIIS database, numbers of invasive alien species show very similar trends over time, but with lower numbers in comparison to established alien species (**Figure 2.4**; Seebens, 2021).

Most studies on selected taxonomic groups, specific regions, or global analyses show systematic and constant increases in established alien animal species across taxonomic groups (e.g., Aukema et al., 2010; Bailey et al., 2020; E. E. Dyer, Redding, et al., 2017; Fuentes et al., 2020; Seebens, Blackburn, et al., 2017). For example, bird and mammal introductions mostly occurred in three distinct phases: first, historically with the discovery and colonization of new lands by Europeans from about 1500 to 1700; second, mainly through acclimatization societies (i.e., associations that encouraged the introduction of alien species), particularly via European colonialism from 1700 to 1900 (e.g., Pipek et al., 2015); and since the 1950s, mostly via global trade (Biancolini et al., 2021; Cassey et al., 2015; E. E. Dyer, Redding, et al., 2017; Hulme, 2021; Turbelin et al., 2017). In contrast to alien homoeotherms, the pet trade is the primary cause of herpetofaunal introductions, a recently spreading group (Capinha et al., 2017). For insects, there are two distinct waves of accelerated introduction rates, one between 1820-1914 and one from 1969 to present, likely due to intensifying global trade and transport (Bonnamour et al., 2021; Roques et al., 2016). Horticulture in general including the trade for ornamental purposes represents an important pathway for the introduction of vascular plants and their pathogens (**Figure 2.2**; Hulme, 2011; van Kleunen et al., 2018). In addition to the total number of introduced alien species, the rate of species accumulation also continuously increased for most taxonomic groups in recent decades (see below), indicating a long-lasting intensification of introductions. Mammals represent the only exception, showing declines in species accumulation rates since about 1950, likely a consequence of stricter regulations on animal trade and husbandry and limited source pools (Seebens et al., 2018; Simberloff et al., 2013).

Once established in a new location, alien species are likely to spread to new areas within the introduced range either by natural dispersal or by means of human-mediated transportation. Approximately 90 per cent of all species introduced before 1700 are found today in more than one region, indicating further spread or multiple introduction events (Seebens, Blackburn, et al., 2021). Spread of an alien species usually lasts for decades to centuries (Gassó et al., 2010; Roques et al., 2016). Rates of inter-regional spread were already high in the nineteenth century for many taxonomic groups, and peaked at that time for vascular plants, but increased further for other taxa, particularly for birds and invertebrates (Seebens, Blackburn, et al., 2021). While spread appears to be slowing for a few already widespread alien species, it is likely that the vast majority of established alien species found currently in only a few sites (Pyšek, Pergl, et al., 2017; Seebens, Blackburn, et al., 2021) will spread also without human assistance in the near future.

The increase in numbers of established alien species is consistent among IPBES regions (**Figure 2.4**). Before 1800, numbers of established alien species rose more rapidly in Europe and Central Asia, although Europe by far has the most records of first year of observations. The differences in early records between Europe and Central Asia and other IPBES regions are likely due to different sampling intensities (Seebens, Blackburn, et al., 2017). In addition, due to time lags (lag phase in the **Glossary**), the rapid increase in researchers studying biological invasions and their impacts, and the subtlety of some impacts, the number of established alien species, and invasive alien species is almost certainly underestimated (Bellard & Jeschke, 2016). The steepest increases in established alien species were observed from post-1850 to the present, particularly for the Americas and the Asia-Pacific regions. These two IPBES regions followed similar trajectories of increases from about 1950 onwards resulting in similar total species numbers in 2005, between 7,000 and 8,000 established alien species for the Americas and the Asia-Pacific regions respectively. Note that the total number of recorded established alien species is higher than shown in the time series due to missing years of first records for most taxa and regions. The number of established alien species for Africa is notably low and markedly different from other regions. This is a general pattern that also holds when species numbers in particular taxonomic groups in Africa are plotted separately (Pyšek, Hulme, et al., 2020). It is not fully understood why numbers are so much lower in Africa, but it is most likely due to Africa having lower imports than other regions, a lack of information on the year of first records of established alien species in Africa, and because the continent is generally understudied in terms of biological invasions (Pyšek et al., 2008; **section 2.4.2**). As classified by GRIIS, numbers of invasive alien species show very similar dynamics though at a lower number, with correlation coefficients of times series over 0.95 for all IPBES regions (**Figure 2.4**). The high correlation between the distribution of established alien species and invasive alien species, which has also been reported in other studies (Pyšek, Pergl, et al., 2017), makes it very likely that trends and status of invasive alien species resemble those of established alien species, noting there are less invasive than established alien species.

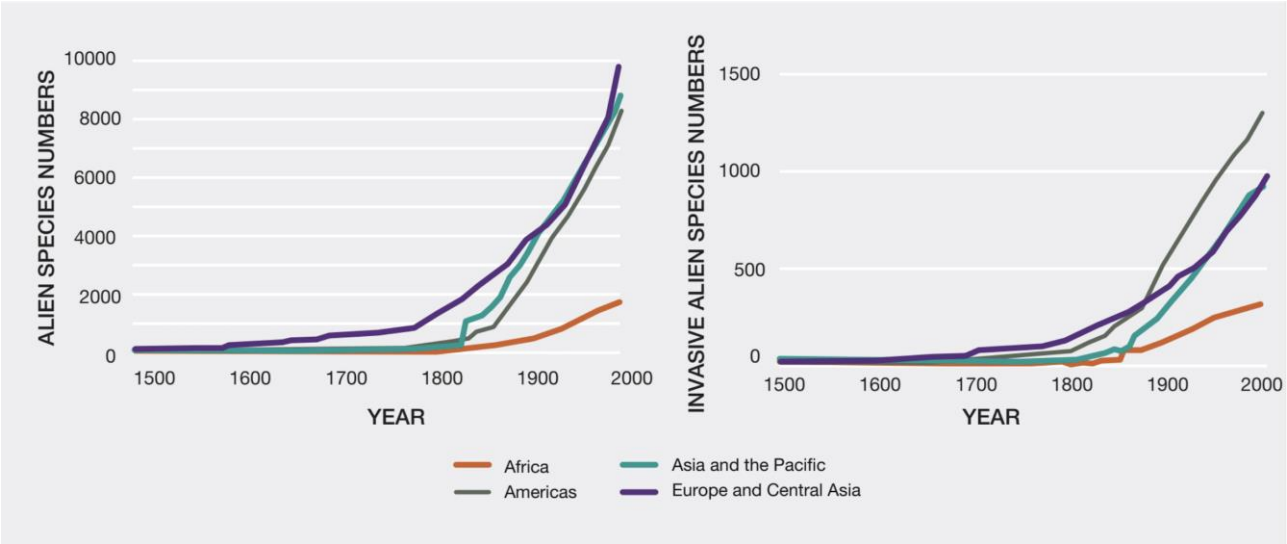

Figure 2.4. Trends in numbers of established alien species and invasive alien species. Total numbers of established alien species (left) and invasive alien species (right) are shown for IPBES regions for 1500-2005. Numbers underestimate the true extent of alien species occurrences due to a lack of data (section 2.1.4 for further details about data processing). A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

2.2.2. Status

According to the chapter database underlying the figures and tables in this chapter, at least 39,215 alien species have been recorded worldwide. As the database does not contain all records of alien species (**section 2.1.4**), the true number is likely much higher. Of those alien species, 37,215 are recorded as having established alien populations, while 5,256 are classified as invasive alien species (**section 2.1.4**). Note that the total number of invasive alien species deviates from the number provided in **Chapter 4** due to different approaches and data sources. As the number of alien species recorded is unequally distributed across the globe (**Figure 2.5**), because the detectable patterns depend upon available data, and because large data gaps remain (**section 2.2.3**), it is in some cases difficult to distinguish data biases and artifacts from true biological patterns. However, with continued research effort, the gaps are gradually shrinking. In the terrestrial and marine realms and consistent across taxonomic groups, the highest numbers of established alien species are found in Europe (particularly western Europe), North America, and Australasia (Dawson et al., 2017). However, total numbers are higher than shown in **Figure 2.4** where only available global databases were included. For many regions, particularly several countries in Africa, Central Asia and many islands, data are scarce and available lists are incomplete. For many marine ecoregions (white areas), alien species occurrence data are lacking or not yet integrated into larger databases (**Figure 2.5**).

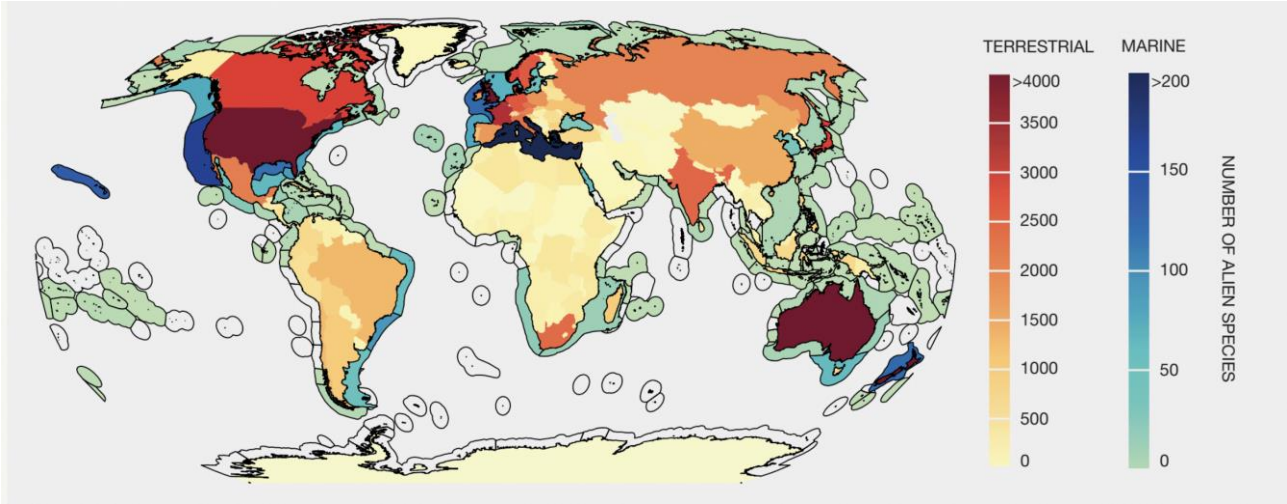

Figure 2.5. Numbers of established alien species per region. The total number of established alien taxa per mainland region (terrestrial and freshwater) and marine ecoregion (marine) is indicated by colour separately. White denotes missing information. Note that marine records were available on different geographic delineations and thus marine ecoregions differ in sizes in this figure. Note that numbers may deviate from those reported in the text due to variation among data sources. See **section 2.1.4** for further details about data sources and data processing. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Global patterns of established alien species distributions were consistently assessed only for selected groups such as ants, spiders, amphibians, reptiles, freshwater fishes, birds, mammals and vascular plants for 186 islands and 423 mainland regions by Dawson et al. (2017). This study showed that established alien species from these groups are unevenly distributed, with some regions (particularly Europe, North America, and Australasia) harbouring more species than other regions. Although Dawson et al. (2017) previously provided the most comprehensive representation of established alien species distributions across taxonomic groups, their assessment included only two invertebrate groups (ants and spiders) and no marine species were included because of the lack of comprehensive information. The analysis by Dawson et al. (2017) based on the seven animal groups revealed two major commonalities: islands and coastal areas have greater proportions of established alien species in regional faunas, and high numbers of established alien species are associated with indicators of human activities such as land-use intensity and trade. The distribution of established alien species varies by taxonomic group. For example, biological invasion hotspots of ants are found in South America, equatorial Africa, and Southeast Asia (Bertelsmeier et al., 2015), while bird and mammal invasions are concentrated in North America, western Europe, South Africa, Japan, Australia, and New Zealand (Biancolini et al., 2021; E. E. Dyer, Cassey, et al., 2017). Numbers of established alien species show latitudinal trends: alien bird species are greatest at mid-latitudes and reflect concomitant variations in human activity, most notably the number of species introduced to a particular location (E. E. Dyer, Redding, et al., 2017). Below, overviews and examples of established alien species are provided for different taxonomic groups (**Tables 2.2**, **2.3**).

The worldwide distribution of established alien species shows a marked latitudinal gradient with the highest species numbers reported at mid-latitudes, such as the temperate regions of the Northern and Southern Hemispheres, with lower numbers in the tropics (Q. Guo et al., 2021; Sax, 2001). The mechanisms that drive this pattern are not yet fully understood but may be positively correlated with invasive alien plant density, the human development index, and the location of most of well-developed countries in temperate regions (Weber & Li, 2008). Greater resistance to biological invasions, faster recovery after disturbance due to higher diversity, lack of life history traits that confer shade tolerance and lower colonization, high predation pressure, and propagule pressures (**Glossary**) are proposed, but not proven, to be major causes of lower alien richness in tropical

continental regions compared to non-tropical regions (Fine, 2002; Freestone et al., 2011; Isbell et al., 2015; Rejmanek & Richardson, 1996). However, on islands the pattern is very different, with tropical islands harbouring very high numbers established alien species (Moser et al., 2018; Rejmanek & Richardson, 1996). Thus, it seems unlikely that tropical regions have a greater resistance to biological invasions compared to non-tropical regions as they lack the characteristics to make them less vulnerable (Chong et al., 2021). However, one explanation for lower numbers of established alien species in tropical regions is lower levels of propagule pressure (i.e., fewer introductions and/or smaller introduction size) due to factors such as low import volumes. In addition, reduced sampling intensities due to lower research efforts and fewer monitoring programmes also likely contribute to the lower numbers recorded in the tropics (Chong et al., 2021).

Table 2.3. Numbers of established alien species for various taxonomic groups worldwide

Species numbers can vary depending on data sources. Note numbers in this table may deviate from those reported in the text due to variation among data sources. For mammals, birds, and vascular plants, ranges of values indicate variation among databases (**section 2.1.4** for further details about data sources and data processing). A data management report for the data underlying this table is available at https://doi.org/10.5281/zenodo.7615582

Taxonomic group	Number of species
Mammals	197-368
Birds	495-877
Fishes	1,451
Reptiles	411
Amphibians	135
Insects	6,795
Arachnids	500
Molluscs	826
Crustaceans	661
Vascular plants	13,081-18,543
Algae	734
Bryophytes	88
Fungi	1,149
Oomycetes	70
Bacteria and protozoans	38

Table 2.4. Top 10 most widespread invasive alien species worldwide

The number of regions where a species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien species and not their impacts, covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Organism group	Taxon	Number of regions
Vascular plant	*Pontederia crassipes* (water hyacinth)	74
Vascular plant	*Lantana camara* (lantana)	69
Mammal	*Rattus rattus* (black rat)	60
Vascular plant	*Leucaena leucocephala* (leucaena)	55

Mammal	*Mus musculus* (house mouse)	49
Mammal	*Rattus norvegicus* (brown rat)	48
Vascular plant	*Ricinus communis* (castor bean)	47
Vascular plant	*Ailanthus altissima* (tree-of-heaven)	46
Vascular plant	*Robinia pseudoacacia* (black locust)	45
Vascular plant	*Chromolaena odorata* (Siam weed)	43

Comprehensive overviews of the global distribution of individual taxonomic groups exist mostly for vascular plants (E. J. Jones et al., 2019; Pyšek, Pergl, et al., 2017) and vertebrates (mammals, birds, amphibians, reptiles and fishes) (Capinha et al., 2017; Dawson et al., 2017; E. E. Dyer, Cassey, et al., 2017; Pyšek, Hulme, et al., 2020), with the exception of a few invertebrate groups such as spiders and ants (Dawson et al., 2017) and land snails (Capinha et al., 2015), and bryophytes (Essl et al., 2013). Patterns of spatial distribution were similar across most taxonomic groups with particularly large numbers of terrestrial alien species in Europe, North America, and Australasia (Dawson et al., 2017). As an exception, there are large numbers of alien fern species in the tropical regions of South America and Asia (E. J. Jones et al., 2019). Common explanations for the variations observed in the spatial distribution of terrestrial alien species include variation in drivers such as trade and transport, GDP, high human population densities, and the degree of disturbance (Capinha et al., 2017; Dawson et al., 2017; E. E. Dyer, Cassey, et al., 2017). Often alien species originate from neighbouring regions or regions connected through trade over long distances (D. S. Chapman et al., 2017; L. Henderson, 2006; Pyšek et al., 2012). High numbers of terrestrial alien species were often found on islands compared to mainlands, with remote islands often showing particularly large alien species numbers (Blackburn et al., 2008; Moser et al., 2018). While it is unknown whether these high numbers can be explained by high propagule and colonization pressures (**Glossary**) due to human activities, or instead are a result of the traits of the native communities, both factors likely interact to affect the outcome of invasions on islands.

2.2.3. Data and knowledge gaps

Perceptions of the distribution of alien species are highly influenced by an unequal global sampling of information on alien species occurrences. For example, hotspots (**Glossary**) of alien species occurrences (i.e., areas of high alien species richness relative to other regions with similar biogeographic characteristics; Dawson et al., 2017) are well-known to coincide with global hotspots of data availability and study sites (L. J. Martin et al., 2012; C. Meyer et al., 2015), shaping knowledge of species distributions (A. C. Hughes et al., 2021). This conclusion is confirmed by the information provided in this chapter: mapping of the number of available studies, which were used to generate the underlying database of this chapter (**section 2.1.4** for further details on the data generation), revealed that regions with high level of information on alien species occurrences (**Figure 2.6**) match the hotspots of established alien species occurrences (**Figure 2.5**). Hence, knowledge of invasive alien species occurrences is biased towards well-sampled regions such as Europe and North America and taxonomic groups such as vertebrates and plants with the majority of studies conducted in recent decades (Bellard & Jeschke, 2016; Jeschke et al., 2012; Pyšek et al., 2008). It remains unclear how much of the distributions of alien species and documented hotspots is affected by spatial variation in research intensity. The investigation of data availability as described in **section 2.1.4** showed extensive data gaps, particularly in large parts of Africa, Central Asia and on islands worldwide (**Figure 2.6**).

In addition to regional biases, research intensities vary across taxonomic groups. There is considerably more information available on the distribution of alien and invasive alien species for vertebrates, particularly mammals (**section 2.3.1.1**), birds (**section 2.3.1.2**), and vascular plants

(**section 2.3.2.1**) than for other taxa. In general, there are large data and knowledge gaps for invertebrates and microorganisms. While most information about invertebrates is available for insects, crustaceans, and molluscs, these data are still incomplete for many regions of the world (**sections 2.3.1.6**, **2.3.1.8**, **2.3.1.9**). Information for other invertebrate groups is extremely scarce. Globally little information is available for alien microorganisms and recorded distributions are often biased towards individual studies. Across realms, the greatest amount of information is available for terrestrial habitats (**section 2.5.1**), while information for aquatic (marine, freshwater and brackish) alien species is often lacking (**sections 2.5.2**, **2.5.3**). Consequently, the lists of alien species for individual regions are, in most cases, incomplete, even for well-sampled regions due to the lack of information about microorganisms and invertebrates, for example, and the degree of incompleteness varies highly among regions globally.

Most of the information about alien species occurrences is available at the national scale for whole countries, while information on sub-national units such as federal states, provinces, protected areas, or private land is usually lacking. Information about occurrences is particularly scarce for lands and waters managed by Indigenous Peoples and local communities (**Box 2.6**). Furthermore, information about abundances and changes in abundances of alien populations is available only in a few cases and is not consistently recorded across regions and taxa. Additional uncertainty in the records of alien and invasive alien species occurrences arises from time delays frequently observed between the actual species introduction and its first record as a new population outside its native range (Crooks, 2005). For vascular plants, these time lags have been estimated to be on average 20 years (Seebens et al., 2015), while for individual cases time delays of up to 150 years have been recorded (Kowarik, 1995b).

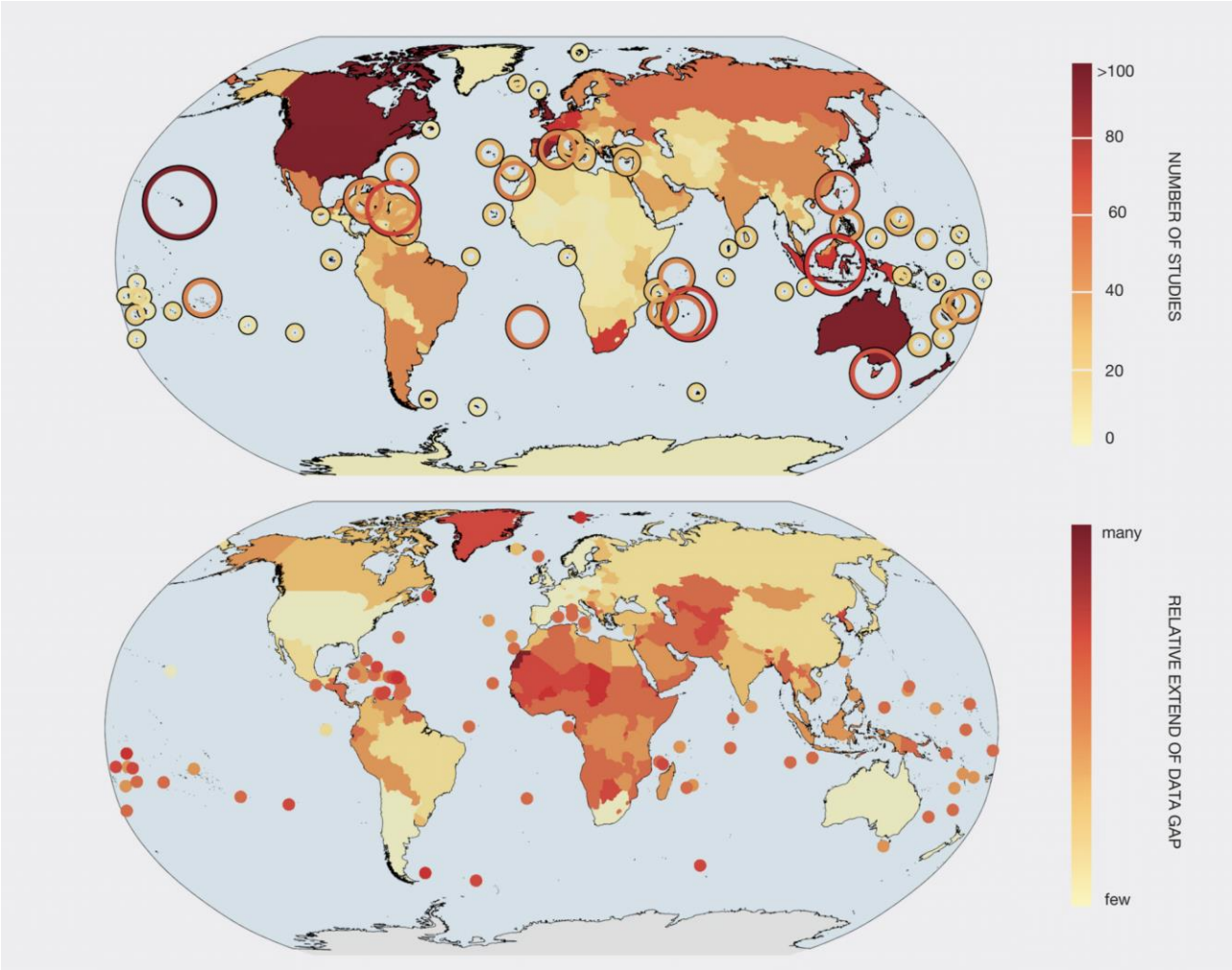

Figure 2.6. Research intensity and data gaps for global established alien species distribution records. Research intensity (top) is indicated by the number of studies available in the chapter database. Data gaps (bottom) were determined as the lack of information for the seven most common phyla as recorded in the chapter database per region. Largest data gaps are apparent in Africa, Central Asia, and for many islands (section 2.1.4 for further details about data sources and data processing for further details of the analysis). Islands are indicated by dots and circles, respectively. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

2.3. Global trends and status of alien and invasive alien species by taxonomic groups

2.3.1. Animals

This section reports on the temporal trends and status of the distribution of alien and invasive alien animal species for various animal groups, namely mammals (**section 2.3.1.1**), birds (**section 2.3.1.2**), fishes (**section 2.3.1.3**), reptiles (**section 2.3.1.4**), amphibians (**section 2.3.1.5**), insects (**section 2.3.1.6**), arachnids (**section 2.3.1.7**), molluscs (**section 2.3.1.8**), crustaceans (**section 2.3.1.9**), and other invertebrates (**section 2.3.1.10**), as well as data and knowledge gaps (**section 2.3.1.11**).

2.3.1.1. Mammals

Trends

Because they were useful, mammals were among the first species introduced by humans, and the first records of introduced alien mammals date back thousands of years (Genovesi et al., 2012). For example, mammals have been used as pack animals, for meat and fur, ornamentals, biocontrol agents, and pets since the expansion of humans from Africa to other continents (Clout & Russell, 2008; Long, 2003; Simberloff & Rejmanek, 2011). During prehistoric and historic human migration, humans transported mammals to new areas to create wild populations for settlers to hunt (Clout & Russell, 2008; Long, 2003; Simberloff & Rejmanek, 2011), peaking with European colonization. As a consequence, there were high numbers of alien mammals as early as 500-200 years ago (**Figure 2.7**). During the nineteenth century, a further acceleration of new records occurred (Biancolini et al., 2021) when specific organizations (i.e., acclimatization societies) focused on alien species release to aesthetically "improve" the landscape and local fauna of colonial territories (Osborne, 2000; Simberloff & Rejmanek, 2011). In recent decades, the dominant pathways of mammal introductions have shifted from hunting and "faunal improvement" to the pet trade likely due to stricter regulations targeting alien mammals (Simberloff et al., 2013). Many mammal introductions outside of their native ranges were also carried out for conservation, and to protect mammal species from overhunting, habitat loss, and invasive alien predators (Biancolini et al., 2021; Seddon et al., 2015; Woinarski et al., 2015).

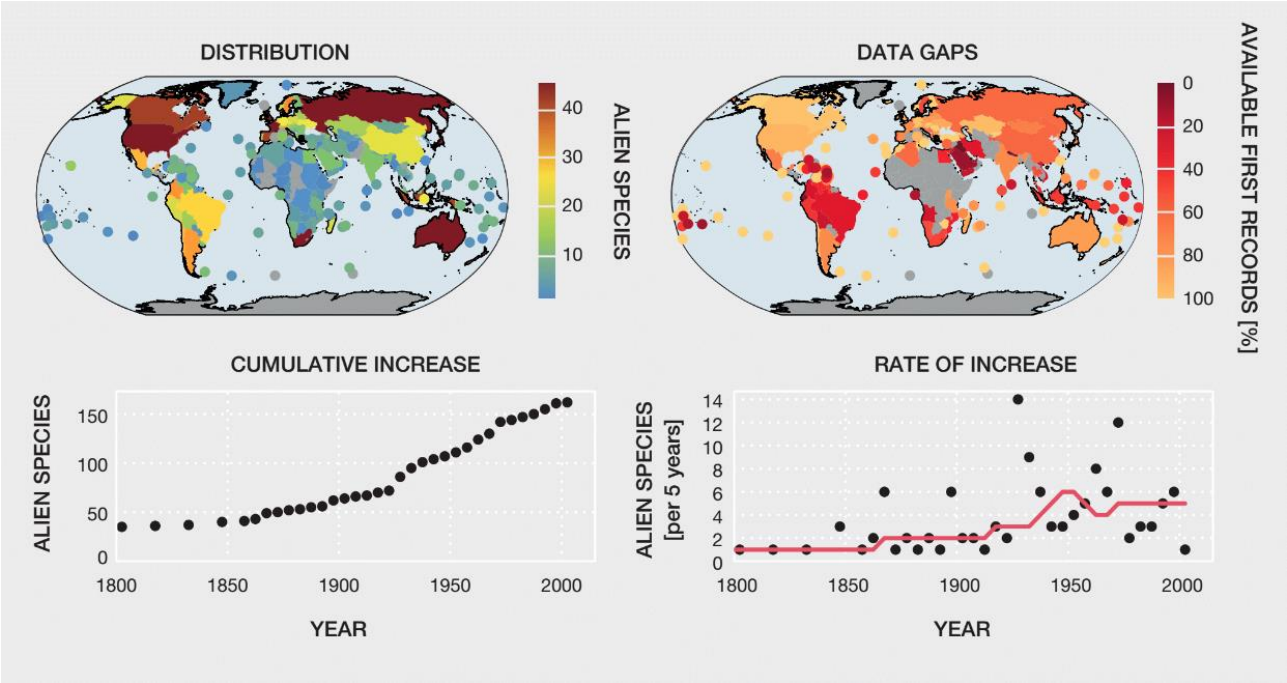

Figure 2.7. Status, trends, and data gaps for established alien mammals. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (section 2.1.4 for further details). Grey regions denote areas with lacking data. Oceans are tinted to aid visualization and do not indicate species numbers. Trends are shown in lower panels as cumulative numbers and as a rate of increase (i.e., numbers of alien species per five years). Smoothed trend (line) is calculated as running median (section 2.1.4 for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

The biological invasion history and status of mammals are among the best documented of alien animal taxa (Biancolini et al., 2021; Blackburn et al., 2017; Clout & Russell, 2008; Long, 2003). At present, 241 mammal species have established alien populations globally, causing many and diverse environmental impacts, especially on insular ecosystems (**Glossary**; Biancolini et al., 2021; Blackburn et al., 2017; Clout & Russell, 2008; **Chapter 4**, **section 4.3.1.1**). If the few records of unsuccessful and unconfirmed introductions are included, at least 274 mammal species have been introduced by humans to new locations (Blackburn et al., 2017; Zenni & Nuñez, 2013).

According to the global Distribution of Alien Mammals database (DAMA), Asia has the highest number of established alien mammals (95), followed by North America (79), Europe (76), Australia (54), Africa (52), Oceania (50), and South America (42) (Biancolini et al., 2021). The major global donors of alien mammal species are Asia (91 established alien species) and Europe (34), Australia (32), North America (31), Africa (30), and South America (23 alien species). An outgoing species flow directed to other continents is predominant for Europe and Asia, while an intracontinental flow (i.e., alien species introduced to other parts of their native continent) is common for Australia (74 per cent of all alien Australian mammals), North America (61 per cent), South America (5 per cent), and Africa (56 per cent). Other countries of Oceania received species only from other continents (Biancolini et al., 2021).

Globally, the vast majority (81 per cent) of alien mammal records are found on islands (Biancolini et al., 2021), most likely due to the higher vulnerability to biological invasions of insular ecosystems and greater propagule and colonization pressure on islands relative to mainland systems (Dawson et al., 2017; Moser et al., 2018). Moreover, alien mammals occur on 97 per cent of islands that harbour highly threatened vertebrate species (Spatz et al., 2017). Among the orders richest in alien mammals, the highest per centage globally is for Rodentia (58 species, 25 per cent), Cetartiodactyla (49 species, 21 per cent), Carnivora (30 species, 13 per cent), Diprotodontia (28 species, 12 per cent) and Primates (26 species, 11 per cent) (Biancolini et al., 2021). Some alien mammals such as *Rattus* spp. (rats), *Mus musculus* (house mouse) and *Felis catus* (cat) are so common that they are often not recognized as invasive alien species in mainland regions (Long, 2003; Loss & Marra, 2017), and thus are missing from lists of alien species. Several of these mammals have lived in close proximity to humans for a very long time resulting in long-lasting commensalisms (Puckett et al., 2020) and in the spread of these species globally.

Many of the most widespread invasive alien mammals worldwide (**Table 2.5**), such as feral domestic species and commensal stowaways, can exploit human-disturbed environments (Biancolini et al., 2021; Long, 2003). On islands and in Australia, where invasive alien mammals are the main cause of extinction and native species declines (Courchamp et al., 2003; Woinarski et al., 2015), they are subject to many control and eradication measures (DIISE, 2020; H. P. Jones et al., 2016; Parkes et al., 2017; Russell et al., 2015, 2016). Other notorious global invasive mammals include *Herpestes javanicus auropunctatus* (small Indian mongoose), *Oryctolagus cuniculus* (rabbits), *Lepus europaeus* (European hare), *Dama dama* (fallow deer), *Camelus dromedarius* (dromedary camel), *Ondatra zibethicus* (muskrat), *Mustela vison* (American mink), *Myocastor coypus* (coypu), *Procyon lotor* (raccoon), *Nyctereutes procyonoides* (raccoon dog), *Vulpes vulpes* (red fox), *Sus scrofa* (feral pig), *Capra hircus* (goats), *Ovis aries* (sheep), *Equus asinus* (donkeys), *Equus caballus* (horse), *Bos taurus* (cattle), and *Canis lupus familiaris* (dogs) (Biancolini et al., 2021; Blackburn et al., 2017; Clout & Russell, 2008; Long, 2003; Louppe et al., 2020). Mammals are the most widespread group of invasive alien animal species in terms of the number of regions invaded (**Table 2.5**).

Table 2.5. Top 10 most widespread invasive alien mammal species worldwide

The number of regions where a species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien mammal species, not impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Taxon	No. of regions	Taxon	No. of regions
***Rattus rattus* (black rat)**	60	*Capra hircus* (goats)	30
***Mus musculus* (house mouse)**	49	*Myocastor coypus* (coypu)	21
***Rattus norvegicus* (brown rat)**	48	*Oryctolagus cuniculus* (rabbits)	20
***Felis catus* (cat)**	38	*Mustela vison* (American mink)	18
***Sus scrofa* (feral pig)**	32	*Canis lupus familiaris* (dogs)	15

2.3.1.2. Birds

Trends

Birds have been introduced for thousands of years, but a notable acceleration of introductions occurred in the mid-nineteenth century arising from increasing European colonial expansion and an acclimatization of alien species considered to be beneficial. The origins and introduction sites of alien birds during this period reflects the geography of colonialism, and the locations of former British colonies (E. E. Dyer, Cassey, et al., 2017), and especially hotspots such as New Zealand, Australia, Hawaii, and the Mascarenes. In this period, alien species were mainly deliberately introduced for game or ornamentation such as gallinaceous birds, wildfowl, and pigeons (E. E. Dyer, Cassey, et al., 2017). Other alien species were introduced for biocontrol of agricultural insect pests such as *Acridotheres tristis* (common myna) introduced from India to Mauritius to control *Nomadacris septemfasciata* (red locust) in 1762 (Shaanker & Ganeshaiah, 1992; Simmonds et al., 1976).

Introduction rates again accelerated in the mid-twentieth century most likely due to increasing trade volumes, particularly for birds imported and exported for the pet trade (**Figure 2.8**). Most recent introductions, reflected in the taxonomic composition, stem from unintentional escapes or releases from the caged bird trade. Commonly introduced species are parrots, estrildid finches, mynas, and starlings (E. E. Dyer, Cassey, et al., 2017).

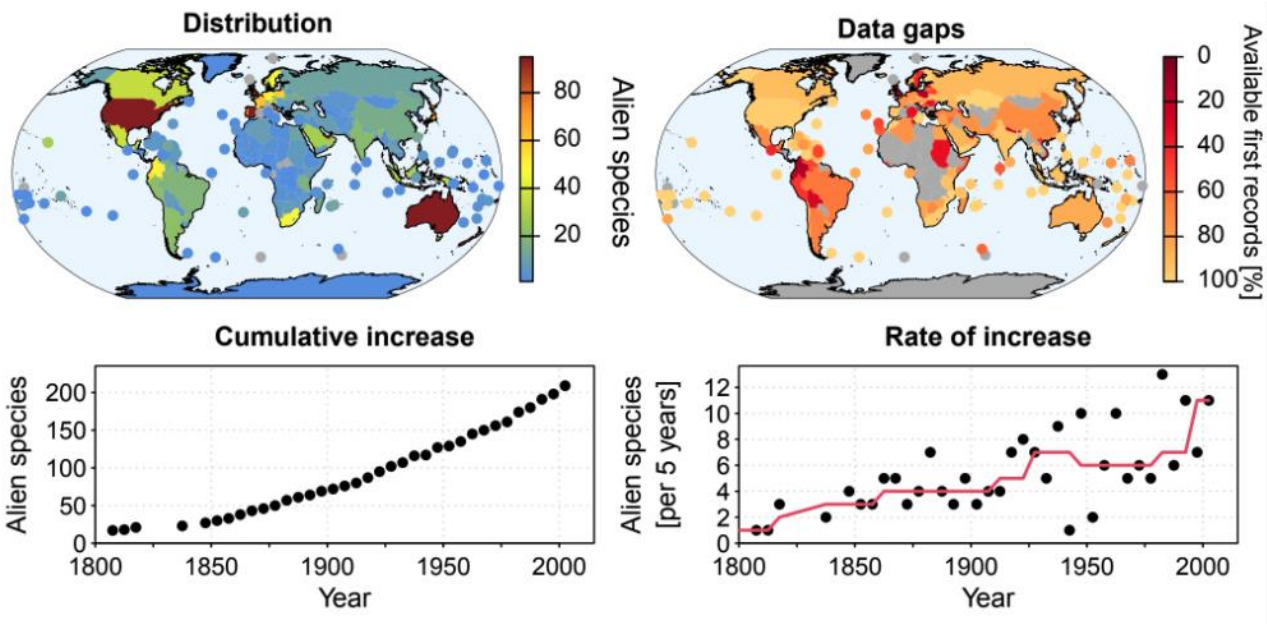

Figure 2.8. Status, trends, and data gaps for established alien birds. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (section 2.1.4 for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (section 2.1.4 for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Alien birds have been introduced to nearly all regions worldwide including many small islands (E. E. Dyer, Cassey, et al., 2017; Evans, 2021). Global patterns of established alien bird species richness show relatively low numbers of alien birds in most parts of the world (though local numbers can be very high, e.g., more than 90 species in Hawaii), but very few regions without established alien bird species (Dawson et al., 2017). E. E. Dyer, Cassey, et al. (2017) showed that colonization pressure (and to a smaller extent, distance from an historic port) was the key driver related to alien bird species richness, and that accounting for these factors, alien bird richness was also higher in areas with high native bird species richness. Thus, a range of environmental, life history, and anthropogenic factors determine areas with high alien bird richness.

A global analysis of historical data on bird introductions showed that environmental conditions at introduction sites are the primary determinants of successful establishment (Redding et al., 2019). While climatic suitability is particularly important, the presence of other alien species can lead to an accumulation of alien species in "hotspots" potentially facilitating the establishment of additional species (termed "invasional meltdown"; **Glossary** and **Chapter 1**, **section 1.3.4**). Establishment of alien species is also more likely when extreme weather events do not occur in the decade following an introduction, suggesting that environmental stochasticity is important to the persistence of small populations (Redding et al., 2019). Species-level traits, notably generalist species and founding population size, exert important secondary effects on success (Redding et al., 2019). Generalist species are more likely to establish self-sustaining populations, as are species introduced in greater numbers (Cassey et al., 2018; Redding et al., 2019). Birds are strong dispersers, a trait that facilitates biological invasion success post-introduction (Cassey et al., 2015). For example, of about 60 pairs of birds first introduced before the twentieth century to Central Park, New York City, *Sturnus vulgaris* (common starling) now numbers approximately 200 million individuals in the United States of America (Linz et al., 2007).

Globally, particularly problematic invasive alien birds include *Anas platyrhynchos* (mallard), *Acridotheres tristis* (common myna), *Pycnonotus jocosus* (red-whiskered bulbul) (Martin-Albarracin et al., 2015), *Nesoenas picturatus* (Madagascar turtle dove), *Pitangus sulphuratus* (great kiskadee), *Tyto novaehollandiae* (Australian masked owl), *Tyto alba* (barn owl), and *Bubo virginianus* (great horned owl) (Evans et al., 2016). The 10 most widespread species are listed in **Table 2.6**.

Table 2.6. Top 10 most widespread invasive alien bird species worldwide

The number of regions where the respective species has been recorded and classified as being invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien bird species, not impacts, which are covered in **Chapter 4** (see **section 2.1.4** for further details on data sources and processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Taxon	No. of regions	Taxon	No. of regions
***Acridotheres tristis* (common myna)**	22	*Branta canadensis* (Canada goose)	9
***Columba livia* (pigeons)**	20	*Alopochen aegyptiaca* (Egyptian goose)	8
***Corvus splendens* (house crow)**	17	*Sturnus vulgaris* (common starling)	8
***Passer domesticus* (house sparrow)**	14	*Myiopsitta monachus* (monk parakeet)	7

***Psittacula krameri* (rose-ringed parakeet)**	13	*Phasianus colchicus* (common pheasant)	6

2.3.1.3. Fishes

Trends

Freshwater fish invasions are one of the best documented biological invasions among animal taxa with considerable information available on invasive alien fish traits, invaded regions, and invasion pathways (Bernery et al., 2022). Information for marine fish invasions is much more fragmented (e.g., Arndt et al., 2018; Vignon & Sasal, 2010). Globally, the number of invasive alien fishes accelerated in the twentieth century (**Figure 2.9**). Although one might conclude that saturation has been reached based on the figure displaying the number of established alien species per five-year intervals, the lag between species introduction, reports of the introduction in the literature, and the cumulative numbers worldwide for this taxonomic group suggest that this is not the case (Seebens, Blackburn, et al., 2017). Even though introductions of fish outside their natural ranges worldwide increased substantially at the onset of the industrial revolution, first records of alien fish introductions date back at least to the Roman Empire in Europe (first and second century; Balon, 1995).

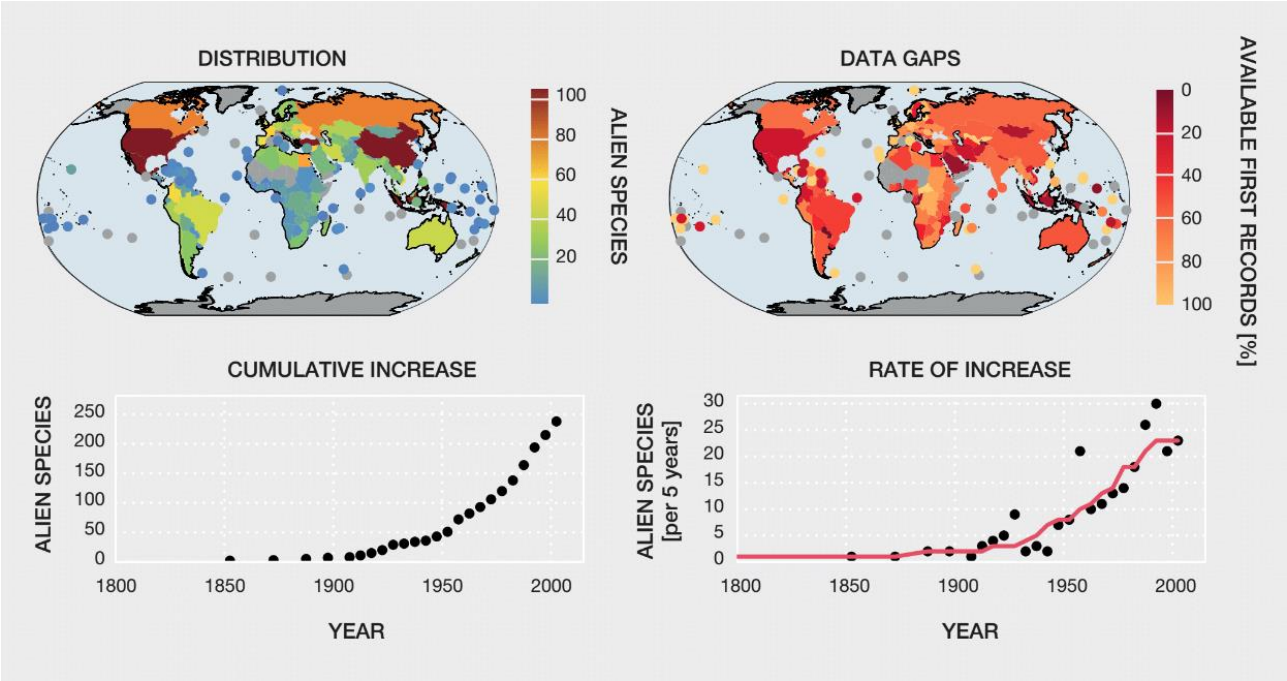

Figure 2.9. Status, trends, and data gaps for established alien fishes. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (section 2.1.4 for further details). Grey regions denote areas with lacking data. Oceans are tinted to aid visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as a running median (section 2.1.4 for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Currently, the rate of newly established alien fish species is still very high, higher than for most other taxa (Seebens, Blackburn, et al., 2017), partially explaining why fish are among the most widespread invasive alien taxonomic group (Gozlan, 2008). Globally, many fish species have been and are often still introduced intentionally, although unintentional introductions also occur. Due to widespread intentional introductions, alien freshwater fish species occur in all biogeographic regions (Leprieur et al., 2008). Due to the compounding effects of increased global maritime transportation, canal construction, and climate change, the number of alien marine fish also rose dramatically in the twentieth and twenty-first centuries. These same three factors may also further promote biological invasions of fish in the future (Castellanos-Galindo et al., 2020; Cohen, 2006; Muirhead et al., 2015; Ruiz et al., 2006).

Status

The most widespread alien fish species are listed in **Table 2.7** demonstrating the very high number of regions invaded by this group, second only to mammals in terms of distribution.

Dawson et al. (2017) showed that alien freshwater fish were distributed in six global biological invasion hotspots where established alien species constituted over 25 per cent of total species richness. When considering within country introductions, which are frequently not included in global analyses, the number of alien fishes increased for large countries such as Brazil, the People's Republic of China, and the United States (Vitule et al., 2019). Pathways of fish biological invasions vary and include inter-oceanic canals, ballast water, intentional introductions for fishing or fisheries stocking, ornamental purposes, and escapes from aquaculture. For example, many alien populations of salmonids, tilapias, and carps originated from aquaculture escapes (Froese & Pauly, 2015). The Center for Food Safety reported about 26 million escaped fish worldwide between 1996 and 2012 (CFS, 2012). Similarly, D. Jackson et al. (2015) reported almost 9 million escapees in six European countries over a 3-year period. Estimates suggest that in Chile more than 1 million salmonids escape annually from the net pens of salmon farms (Sepúlveda et al., 2013; Thorstad et al., 2008). Marine waters are also inhabited by many alien fishes. The opening of the Suez Canal has enabled the migration of species from the Red Sea into the Mediterranean Sea (known as Lessepsian/Erythraean invasion), which has caused the influx of more than 400 Indo-Pacific species into the Mediterranean Sea, including over 100 (118 by latest tally, unpublished) fish species (Bariche & Fricke, 2020; Çinar et al., 2021; Galil et al., 2021b), resulting in considerable changes to fish communities and fisheries, particularly in the Levant basin to date (Arndt et al., 2018; Arndt & Schembri, 2015; Galil et al., 2007). Both *Pterois volitans* (red lionfish) and *Pterois miles* (lionfish) have invaded large areas of the north-western Atlantic imposing large impacts on prey populations of native species and local fisheries (Côté et al., 2013), and *Pterois miles* is now spreading within the Mediterranean Sea (Poursanidis et al., 2020). Species of peacock basses (genus *Cichla*), native to South America, have been introduced to tropical and sub-tropical regions worldwide for fisheries (Franco et al., 2022).

Table 2.7. Top 10 most widespread invasive alien fish species worldwide

The number of regions where the top 10 most widespread fishes have been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien species rather than impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Taxon	No. of regions	Taxon	No. of regions

***Cyprinus carpio* (common carp)**	43	*Poecilia reticulata* (guppy)	22
***Gambusia holbrooki* (eastern mosquitofish)**	42	*Pseudorasbora parva* (topmouth gudgeon)	22
***Oreochromis niloticus* (Nile tilapia)**	28	*Gambusia affinis* (western mosquitofish)	19
***Oreochromis mossambicus* (Mozambique tilapia)**	25	*Lepomis gibbosus* (pumpkinseed)	19
***Oncorhynchus mykiss* (rainbow trout)**	23	*Micropterus salmoides* (largemouth bass)	18

2.3.1.4. Reptiles

Trends

The introduction of alien reptiles has a long history associated with the movement of humans and trade routes. For example, introduced species such as *Tarentola mauritanica* (common wall gecko) and *Vipera aspis* (asp viper) in the Mediterranean Basin can be traced back to the fourth century B.C. and the fifth century, respectively (Masseti & Zuffi, 2011; Mateo et al., 2011; Pleguezuelos, 2002). Since 1800, the number of first records of alien reptiles globally has been rising steadily, accelerating since 1950 (Capinha et al., 2017; Kraus, 2009). Similar trends have also been reported at local and regional scales (Krysko et al., 2011, 2016; Mateo et al., 2011; Perella & Behm, 2020; Powell et al., 2011; Toomes et al., 2020). Most alien reptile introductions through the end of the twentieth century were due to the unintentional transport of species as stowaways or contaminants (Kraus, 2009; Lever, 2003). This pathway remains important, but the pet trade has also emerged as a significant source of alien reptiles in recent decades (É. Fonseca et al., 2019; Lockwood et al., 2019; Perella & Behm, 2020; Stringham & Lockwood, 2018; Van Wilgen et al., 2010).

Contemporary trends (**Figure 2.10**), the expected increase in pet trade as a source of new species, and model-based projections of future distributions all indicate that both the number of alien reptiles and the number of invaded areas will continue to increase (Chapple et al., 2016; da Rosa et al., 2018; Filz et al., 2018; Gippet & Bertelsmeier, 2021; X. Li et al., 2016; X. Liu et al., 2014; Seebens, Blackburn, et al., 2017). Alien reptiles are fast becoming an important group of alien vertebrates alongside other taxa such as birds and mammals. In Australia, alien reptiles have been the dominant group of alien terrestrial vertebrates intercepted and detected at large since 1999 (Toomes et al., 2020).

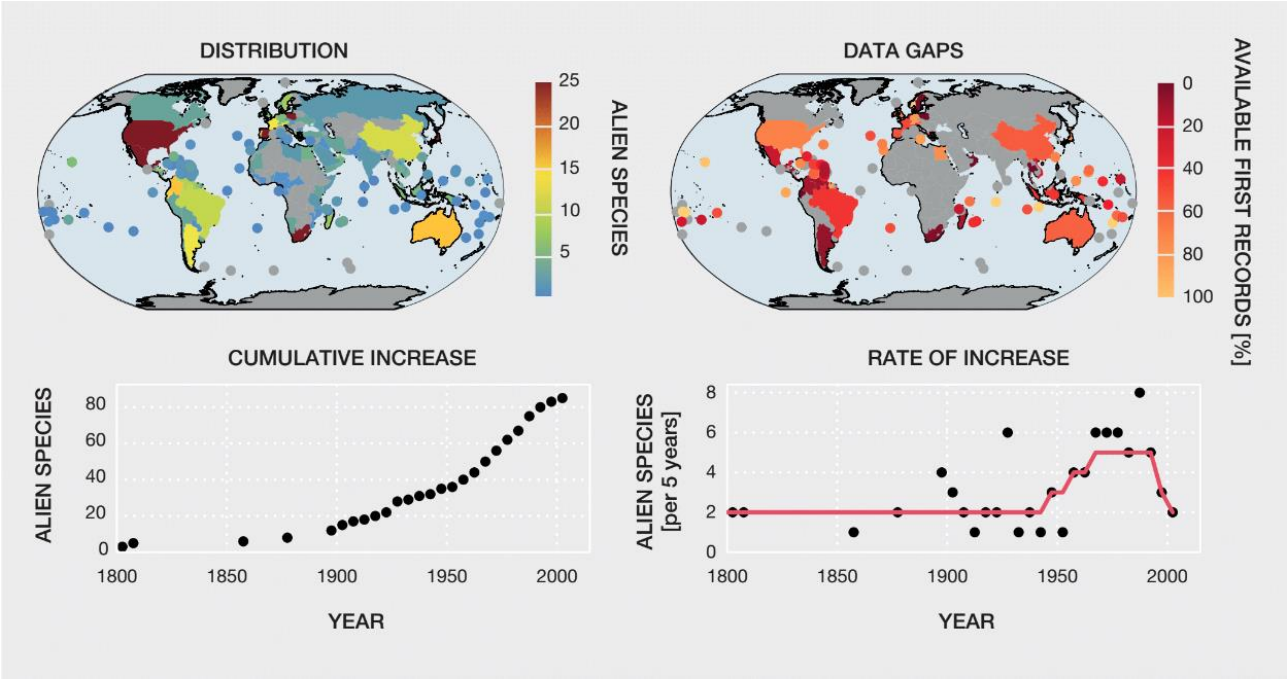

Figure 2.10. Status, trends and data gaps for established alien reptiles. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (section 2.1.4 for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization purposes and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (section 2.1.4 for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Established populations of alien reptiles are found in all the IPBES regions except for the polar areas (Capinha et al., 2017; Kraus, 2009). Islands and areas with relatively warm climates and high economic and human activity tend to host more alien reptiles than other places (Capinha et al., 2017; É. Fonseca et al., 2019; Moser et al., 2018; Silva-Rocha et al., 2019). Of the top five global hotspots for alien reptiles, the top three are in North America (Florida, Hawaii, and California), Europe (Balearic Islands, Spain), and Japan (Capinha et al., 2017; Krysko et al., 2011, 2016; Mateo et al., 2011; Meshaka, 2011; Silva-Rocha et al., 2015).

At least 198 reptile species belonging to three major reptile orders (Squamata, Crocodilia, and Testudines) have established alien populations worldwide (Capinha et al., 2017). Of the top five most commonly established alien reptiles, four species (*Indotyphlops braminus* (brahminy blind snake), *Hemidactylus frenatus* (common house gecko), *Hemidactylus mabouia* (tropical house gecko), and *Hemidactylus turcicus* (Mediterranean house gecko)) have been transported unintentionally, and one (*Trachemys scripta* (pond slider)) is common in the pet trade (Capinha et al., 2017; García-Díaz et al., 2015; Kraus, 2009; Masin et al., 2014). Some of the above species are among the 10 most widespread of all invasive alien reptiles worldwide (**Table 2.8**). The establishment success and spread rates of alien reptiles are associated with high propagule pressure, the degree of climate matching between native and recipient regions, presence of congenerics, and high reproductive output (W. L. Allen et al., 2017; Bomford et al., 2009; X. Liu et al., 2014; Mahoney et al., 2014; Tingley et al., 2016; Van Wilgen & Richardson, 2012).As examples, *Python*

bivittatus (Burmese python) is spreading in the Florida Everglades, preying upon many species including the apex native predator *Alligator mississippiensis* (American alligator; Dorcas et al., 2012). Invasive alien *Boiga irregularis* (brown tree snake) has reached iconic status as one of the most impactful invasive alien species worldwide. Fewer than 10 individuals were unintentionally introduced from the United States into the Pacific Island of Guam following World War II (Richmond et al., 2015). This species has since colonized all habitats on Guam, from grasslands to forests, with peak densities as high as 10,000 individuals per km^2 (Rodda et al., 1992). Several lesser known and potentially invasive alien reptiles are emerging including *Varanus niloticus* (Nile monitor) in Florida, *Lampropeltis getula* (common kingsnake) in the Canary Islands, *Boa constrictor* (boa constrictor) on Aruba, and several giant constrictor snakes in Puerto Rico (Reed & Kraus, 2010).

Table 2.8. Top 10 most widespread invasive alien reptile species worldwide

The table shows the number of regions where the species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table refers only to the distribution of invasive alien species, not their impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	No. of regions	Species	No. of regions
***Trachemys scripta elegans* (red-eared slider)**	15	*Chelydra serpentina* (common snapping turtle)	4
***Hemidactylus frenatus* (common house gecko)**	12	*Anolis cristatellus* (Puerto Rican crested anole)	4
***Hemidactylus mabouia* (tropical house gecko)**	12	*Anolis porcatus* (Cuban green anole)	3
***Iguana iguana* (iguana)**	8	*Hemidactylus turcicus* (Mediterranean house gecko)	3
***Anolis sagrei* (brown anole)**	5	*Pelodiscus sinensis* (Chinese soft-shelled turtle)	3

2.3.1.5. Amphibians

Trends

Alien amphibian introductions are not a new phenomenon. For instance, the introduction of *Bufotes balearicus* (Balearic green toad) to the Balearic Islands, Spain, is assumed to have occurred around the second century B.C. (Mateo et al., 2011; Pleguezuelos, 2002). However, the accumulation of first records of alien amphibians shows a global rise since 1800 with a slightly more pronounced increase after the 1950s (Capinha et al., 2017; Kraus, 2009, 2011). Similar patterns of relative increases in both the number of new alien species and the number of records of alien amphibians have been reported regionally and locally (Krysko et al., 2011, 2016; Mateo et al., 2011; Powell et al., 2011; Toomes et al., 2020). Nevertheless, the implementation of biosecurity and rapid response activities in countries such as New Zealand and Australia has likely prevented new introductions and establishment of alien amphibians (Chapple et al., 2016; García-Díaz et al., 2017; Toomes et al., 2020). The United States appears to be an outlier in terms of new introductions; both the number of alien amphibian species reported annually and the number of records per year have

remained relatively stable since around the mid-twentieth century (Mangiante et al., 2018). It is important to note that in 2016 the United States Fish and Wildlife Service published an interim rule listing 201 salamander species as injurious wildlife under the Lacey Act to prevent the arrival of *Batrachochytrium salamandrivorans* (chytrid fungus) carried by alien species in the trade. Similarly, in 2017, Canada restricted salamander importation for the same reason (Yap et al., 2017).

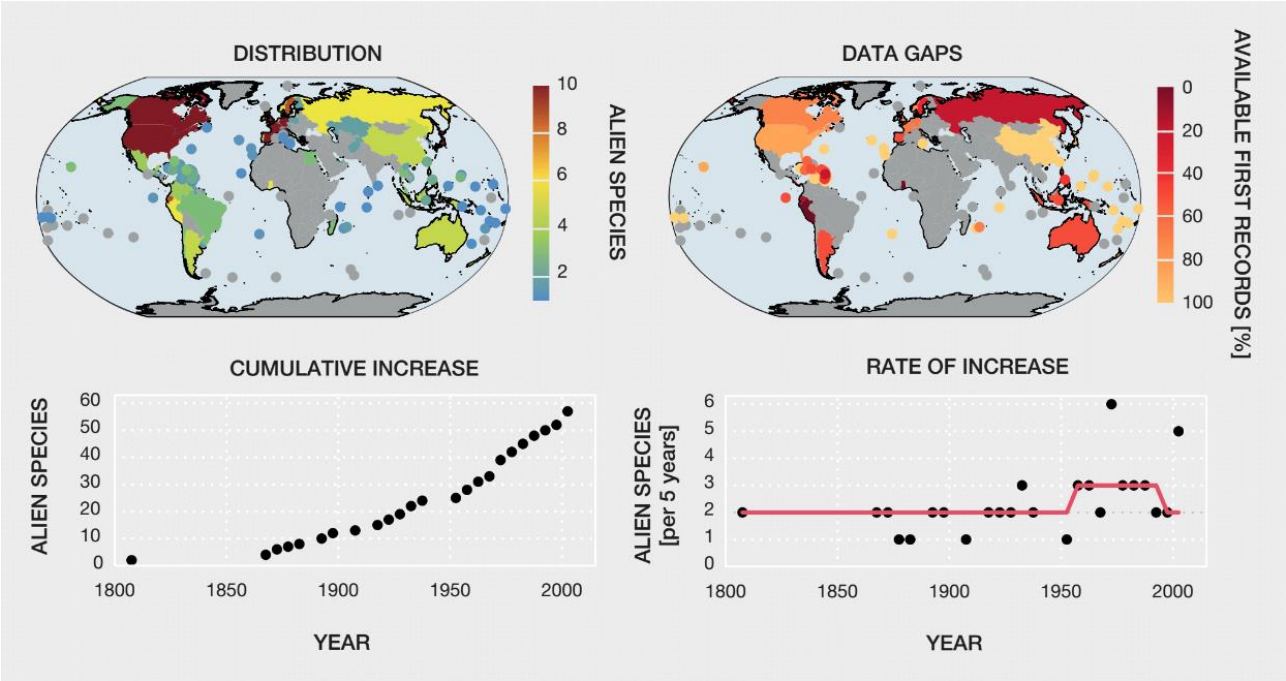

Figure 2.11. Status, trends, and data gaps for established alien amphibians. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (section 2.1.4 for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization purposes and do not indicate species numbers. The trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend line is calculated as running median (section 2.1.4 for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Intentional and unintentional pathways are virtually equivalent contributors to the current distribution and status of alien amphibians worldwide, but their role varies by region and period (Kraus, 2009; Lever, 2003). For example, individuals of several toad species (family Bufonidae), such as *Rhinella marina* (cane toad) and *Sclerophrys gutturalis* (guttural toad), were deliberately released as biocontrol agents in the Indo-Pacific and Caribbean islands during the first half of the twentieth century (Kraus, 2009; Lever, 2003; Powell et al., 2011; Shine, 2018; Telford et al., 2019). More recently, *Duttaphrynus melanostictus* (Asian common toad) has been unintentionally transported to many areas in the Indo-Pacific region (Mo, 2017; Moore et al., 2015; Tingley et al., 2018; Vences et al., 2017). The two most widespread alien amphibians in the world, *Lithobates catesbeianus* (American bullfrog) and *Rhinella marina*, have been introduced as a source of food and for biocontrol purposes, respectively (Capinha et al., 2017; Kraus, 2009; X. Liu et al., 2012, 2015; Shine, 2018). In Australia, almost twice the number of alien amphibians was found introduced through the pet trade compared to the stowaway pathway (71 and 38, respectively), yet the latter is a more important pathway when considering the total number of individuals moved

rather than the number of species (García-Díaz & Cassey, 2014; Toomes et al., 2020). Unintentional pathways are responsible for 12 out of 13 alien amphibians present in Guam (Christy, Clark, et al., 2007). The pet trade is expected to remain a prominent source of new alien amphibian introductions in the near and medium-term (Lockwood et al., 2019; Mohanty & Measey, 2019; Stringham & Lockwood, 2018).

The diversity of transport pathways responsible for the introduction of alien amphibians has resulted in established alien amphibian populations in all IPBES regions except for polar areas (**Figure 2.11**; Capinha et al., 2017; Christy, Savidge, et al., 2007; É. Fonseca et al., 2019; García-Díaz & Cassey, 2014; Kraus, 2009; Measey et al., 2017; Rago et al., 2012; Tingley et al., 2010).The United Kingdom, and California, Hawaii, and Puerto Rico (United States) are the top-four global hotspots of alien amphibians, each with more than five species established (Capinha et al., 2017; Kraus, 2009; Powell et al., 2011). Alien amphibian richness tends to be higher on islands and in places with high precipitation, high potential evapotranspiration, and high levels of economic activity (Capinha et al., 2017; É. Fonseca et al., 2019; Poessel et al., 2012). High propagule pressure, the presence of congeneric species, life-history traits related to rapid growth and reproduction, and environmental similarity between the recipient and the native ranges are associated with the establishment success and invasion rates of alien amphibians (W. L. Allen et al., 2017; Bomford et al., 2009; Ferreira et al., 2012; K. Li et al., 2016; X. Liu et al., 2014; Poessel et al., 2012; Rago et al., 2012; Tingley et al., 2010, 2011; Van Wilgen & Richardson, 2012). It is interesting to note that many species native to Southern Africa have been introduced elsewhere, while few alien amphibians are reported for Southern Africa due to a very low trade involving these animals (Measey et al., 2017).

The reported trajectories, combined with invasive alien amphibian niche shifts and the increase in pet trade, point to future increases in both the number of new alien amphibians and the number of regions occupied (Capinha et al., 2017; Chapple et al., 2016; da Rosa et al., 2018; Mohanty et al., 2021; Mohanty & Measey, 2019; Pili et al., 2020; Toomes et al., 2020). Additionally, invasion debts (i.e., the additional area an invasive alien species is likely occupy in the future; **Glossary**) mean that the accelerating trends in introductions described above could lead to established populations unless rapid response management actions are taken (Chapple et al., 2016; M. J. Spear et al., 2021).

Notorious invasive amphibians include *Rhinella marina* (cane toad), a large and toxic toad native to Mesoamerica and introduced worldwide into sugar cane producing regions to control beetles causing crop damage (Shanmuganathan et al., 2010). *Xenopus laevis* (African clawed frog) is among the most commonly used laboratory animals (e.g., basic biology and formerly for pregnancy testing); many populations originating from laboratories have become invasive in regions with a Mediterranean climate. **Table 2.9** lists the 10 most widespread invasive alien amphibians and the number of regions each has invaded.

Table 2.9. Top 10 most widespread invasive alien amphibian species worldwide

The table shows the number of regions where the respective species has been recorded and classified as being invasive based on GRIIS (Pagad et al., 2022). Note that this table only refers to the distribution of invasive alien species rather than their impacts, which is covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	No. of regions	Species	No. of regions
Lithobates catesbeianus	24	*Pelophylax ridibundus*	3

(American bullfrog)		(Eurasian marsh frog)	
***Rhinella marina* (cane toad)**	14	*Duttaphrynus melanostictus* (Asian common toad)	2
***Xenopus laevis* (African clawed frog)**	9	*Eleutherodactylus coqui* (Caribbean tree frog)	2
***Triturus carnifex* (Italian crested newt)**	3	*Eleutherodactylus planirostris* (greenhouse frog)	2
***Eleutherodactylus johnstonei* (whistling frog)**	3	*Andrias davidianus* (Chinese giant salamander)	1

2.3.1.6. Insects

Trends

Since Insecta is the largest animal class it comes as no surprise that global numbers of alien insect species vastly exceed numbers for all other animal taxa combined by 1.7 times (Seebens, Blackburn, et al., 2017). Yet, their biological invasions are still likely underreported as insects are less studied relative to other organisms such as vertebrates.

While there are a few rare documented cases of natural intercontinental insect spread (e.g., via wind) (Hoffmann & Courchamp, 2016), the long-distant spread of alien insects has risen steeply due to the facilitation by recent human activities (Gippet et al., 2019; Meurisse et al., 2019). Early exploration and colonial settlements facilitated the global range extension of several insect species, but higher rates of alien species establishment did not begin until approximately 1820 and lasted until 1914. This was followed by a second wave of accelerated establishment post-1960 (Bonnamour et al., 2021). These periods coincided with the industrial revolution; increased global trade and travel facilitated accidental movement of insects with plants, plant products, general cargo, and baggage (Bertelsmeier et al., 2017; Bonnamour et al., 2021). Much of the global distribution of alien insects is driven by plant biological invasions (**Chapter 3**, **section 3.3.5.1**); many insects are dependent on individual plant species or genera, so establishment of alien plant species provides necessary resources that facilitate insect establishment (Liebhold et al., 2018). Some evidence indicates that the recent implementation of biosecurity practices has reduced the proportion of imports contaminated with insects (Leung et al., 2014; Liebhold & Griffin, 2016), but imports have also simultaneously and massively increased at the same time. While insects are such a large group that some specific variation may be masked, the resulting trend is a net increase. Indeed, as a group, they have even exponentially increased since the start of the nineteenth century, both in terms of cumulative numbers and number of established alien species per five-year intervals (**Figure 2.12**), and still show no sign of saturation (Bonnamour et al., 2021; Seebens, Blackburn, et al., 2017). The continued increase of global trade and climate change will likely further accelerate for these easily transported and climate-sensitive organisms (Bellard, Thuiller, et al., 2013). Additional factors could contribute to further spread (e.g., large infrastructure projects; Galil, Boero, Campbell, et al., 2015; X. Liu et al., 2019; Muirhead et al., 2015) or establishment (e.g., industrial rearing of insects for food; Bang & Courchamp, 2021) of both existing and new invasive alien insects.

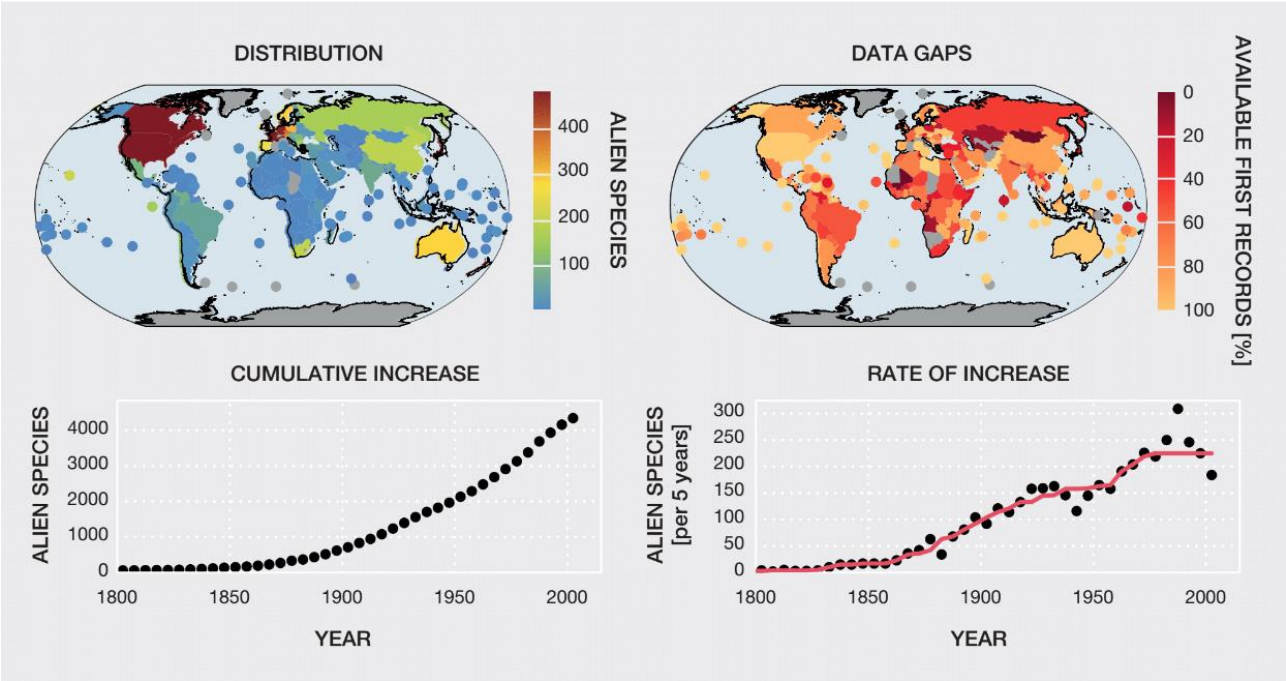

Figure 2.12. Status, trends, and data gaps for established alien insects. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (**section 2.1.4** for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization purposes and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (**section 2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Global estimates of the total number of alien insects are not available but likely exceed 10,000 species with more than 3,500 species established in North America alone (Yamanaka et al., 2015). Actual numbers are likely much higher since many established species remain undiscovered or unreported. Global hotspots of insect biological invasions appear to be related to historical patterns of urbanization and industrialization (Branco et al., 2019; Huang et al., 2011) and the transport of species between Europe, East Asia, and North America reflecting trade and travel patterns (Kenis et al., 2007; Mattson et al., 2007). As global connectivity increases, regions such as Africa and South America are likely to be increasingly important as both recipients and donors of invasive alien insects.

Many invasive alien insects are highly problematic around the world, with coleopterans, lepidopterans, dipterans, and hymenopterans being among the most notorious (e.g., Kenis et al., 2009). For example, alien ant species are often considered among the worst invasive alien species (Holway et al., 2002; Pyšek et al., 2008). Three ants are among the 10 most widespread invasive insects (**Table 2.9**) and five are among the "100 of the world's worst invasive alien species", the only family to have so many species listed. Ants are easily transported by humans because of their generalist nesting habits and their small size (Wetterer et al., 2009). When intercepted at ports of entry, alien ant species are frequently detected on commercial ornamental plants (Lester, 2005; Suarez et al., 2005; Ward et al., 2006). Globally, more than 200 species have established

populations outside their native distributions (Wetterer et al., 2009), but over 600 species have likely been introduced outside their native ranges (Miravete et al., 2014). This makes ants the most represented insect family and particularly notorious ant species include *Linepithema humile* (Argentine ant), *Anoplolepis gracilipes* (yellow crazy ant), *Wasmannia auropunctata* (little fire ant), *Solenopsis invicta* (red imported fire ant), and *Pheidole megacephala* (big-headed ant). In addition, a recent study predicted that 13 other species with similar ecological traits could also become invasive should they be introduced outside their native ranges (Fournier et al., 2019). To date, few studies are available on the biology and ecology of these invasive alien ants, except for *Linepithema humile* and *Solenopsis invicta* (Bertelsmeier et al., 2016; Pyšek et al., 2008). These two ant species from South America have invaded many countries by separate multiple introductions from their native ranges and subsequent secondary spread from invaded ranges (Ascunce et al., 2011; Giraud et al., 2002). Secondary introduction seems to be common for ants: 76 per cent of interception events of alien ants at the border of the United States and 88 per cent of those intercepted at the New Zealand border did not come from their country of origin but from previously invaded countries (Bertelsmeier et al., 2018).

Many alien insects are invasive in most parts of the world making it difficult to define the most important while remaining concise, but the 10 most widespread species provide good examples (**Table 2.10**). *Ceratitis capitata* (Mediterranean fruit fly) and *Bemisia tabaci* (tobacco whitefly) affect agriculture in numerous countries, while insect-borne diseases are spread by the invasions of several mosquito species, such as *Aedes albopictus* (Asian tiger mosquito), *Aedes aegypti* (yellow fever mosquito), and *Anopheles quadrimaculatus* (common malaria mosquito). *Harmonia axyridis* (harlequin ladybird) was introduced to North America and Europe to control aphids, subsequently leading to the decline of native ladybirds through predation (Roy et al., 2012). *Icerya purchasi* (cottony cushion scale) is found in most regions, where it feeds on more than 80 families of woody plants, particularly citrus crops. *Brontispa longissima* (coconut hispine beetle) feeds on young leaves of coconut palms throughout the Pacific region. *Bemisia tabaci* thrives in tropical and subtropical (and to a lesser degree temperate) regions, where it feeds on many plants but also facilitates the spread of plant viruses. Although not among the 10 most widespread, some other insects are among the best known of all invasive alien species. For example, North American forests have been deeply damaged by the invasions of *Agrilus planipennis* (emerald ash borer; Herms & McCullough, 2014; Poland & McCullough, 2006; Valenta et al., 2017), *Anoplophora glabripennis* (Asian longhorned beetle; Dodds & Orwig, 2011; Kappel et al., 2017; Nowak et al., 2001), and *Lymantria dispar* (gypsy moth; C. B. Davidson et al., 1999; Tobin et al., 2012). *Drosophila suzukii* (spotted wing drosophila), a vinegar fly of Asian origin, has emerged as a devastating pest of small and stone fruits throughout North America, Europe and South America (L. A. dos Santos et al., 2017). *Coptotermes formosanus* (Formosan subterranean termite) affects infrastructure and *Trogoderma granarium* (khapra beetle) destroys grain and seed reserves throughout the world. It is noteworthy that bees (*Apis* (honey bee), *Bombus* (bumble bee) or *Megachile* (leaf-cutter bees), among others; e.g., Bartomeus et al., 2013; Goulson, 2003; Morales et al., 2017) and wasps (*Vespa*, *Vespula*, gall and parasitoid wasps, among others; e.g., Beggs et al., 2011; Lester & Beggs, 2019) excepting *Apis mellifera scutellata* (Africanized bee), hybrid of several European honey bee subspecies and the East African honey bee, are the source of considerable revenue and rarely viewed as invasive despite outcompeting native pollinators (IPBES, 2016; Moritz et al., 2005).

Table 2.10. Top 10 most widespread invasive alien insect species worldwide

The number of regions where the species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table refers only to the distribution of invasive alien species, not their impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed

occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	No. of regions	Species	No. of regions
Icerya purchasi **(cottony cushion scale)**	29	*Harmonia axyridis* (harlequin ladybird)	14
Tapinoma melanocephalum **(ghost ant)**	28	*Ceratitis capitata* (Mediterranean fruit fly)	14
Pheidole megacephala **(big-headed ant)**	24	*Brontispa longissima* (coconut hispine beetle)	13
Aedes albopictus **(Asian tiger mosquito)**	24	*Bemisia tabaci* (tobacco whitefly)	13
Solenopsis geminata **(tropical fire ant)**	19	*Cameraria ohridella* (horsechestnut leafminer)	13

2.3.1.7. Arachnids

Trends

The number of recorded alien spiders has been increasing continuously (**Figure 2.13**; Nentwig, 2015; Seebens, Blackburn, et al., 2017). An accelerated increase is observed after 1950 similar to those in many other invertebrate groups and likely as a consequence of increasing global trade and transport. In addition to the total number of alien spiders, the rate of annual new records has increased until the present reaching about 30 new records per five years (i.e., 6 new records annually (**Figure 2.13**).

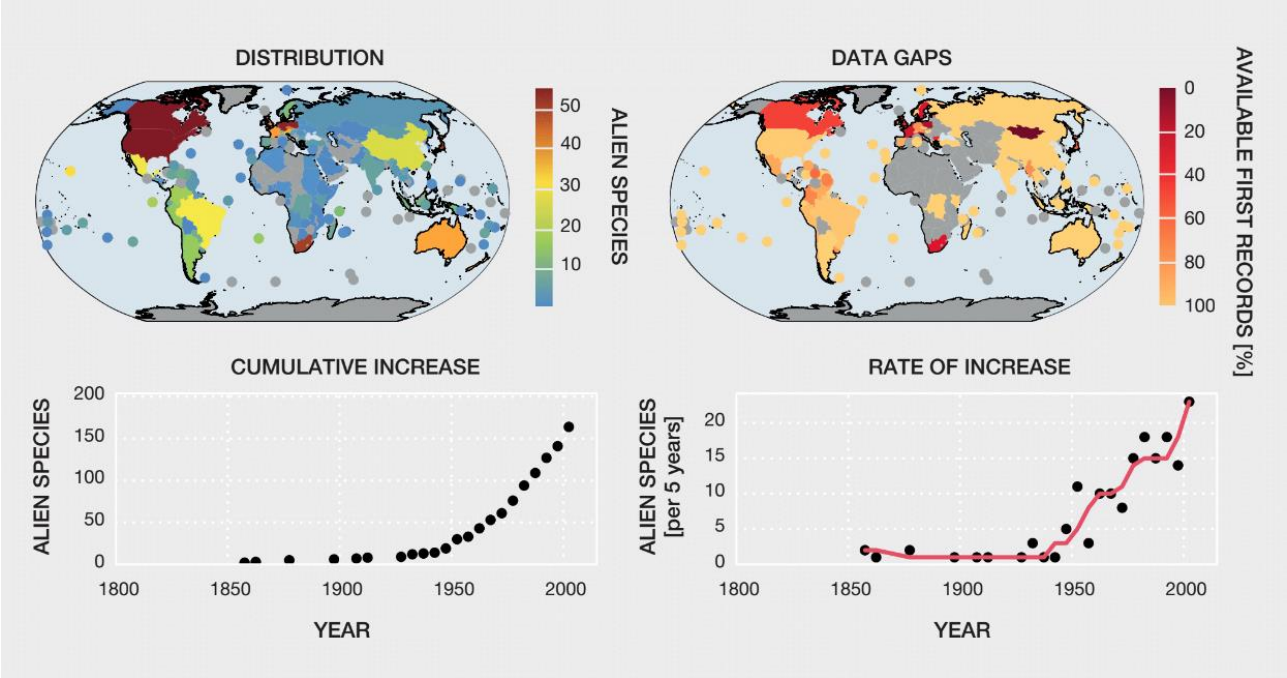

Figure 2.13. Status, trends, and data gaps for established alien arachnids. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (section 2.1.4 for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (section 2.1.4 for further details about data sources and data processing). Note presented

numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Worldwide, 285 alien spider species (0.57 per cent of all described spider species) have been recorded outside of their native range. Most alien spiders are known from only a few records, from a few regions, but some species are so widespread that they are alien to several continents (**Table 2.11**). The 28 most widespread species (10 per cent of all alien spiders) are known from more than 30 invaded regions (often from all or most continents) and represent 50 per cent of all records. Major trade routes, at least past routes, connect areas of origin to invaded regions: 29 per cent of all globally spread spider species are native to Europe (while Europe is home to only 10 per cent of all spider species), 25 per cent from the Americas, 20 per cent from Asia, 17 per cent from Africa, 10 per cent from Australasia and the Pacific. Most spiders alien to Europe were unintentionally introduced either as stowaways, in or on transport vectors (i.e., the physical means or agent that transports a species; **Glossary**), or as contaminants (Nentwig, 2015). Horticulture is a major source of introduced spiders, followed by fruit and vegetable shipments, containers, and packaging materials. Imported classic cars and used sport cars often contained *Latrodectus mactans* (black widow spider) and cocoons in high numbers (Van Keer, 2010). For many areas in the world, no reliable species inventories are available. The top 10 most widespread invasive alien arachnids as recorded by GRIIS are shown in **Table 2.12**.

Table 2.11. The most common established alien spider families and species

Based on 12 arachnid families with the most widely distributed established alien species, this family-wise presentation is of those species known to occur in more than 30 regions outside their native ranges. Families are ordered alphabetically, species according to frequency in the invaded area. Data from the World Spider Catalog (2017).

Family	No. of established alien species	Most widespread species	Alien range
Agelenidae (funnel web spiders)	8	*Tegenaria domestica* *Eratigena agrestis*	Europe Europe
Araneidae (orb weavers)	23	*Neoscona nautica* *Argiope trifasciata*	Pacific North America
Cheiracanthiidae (yellow sac spiders)	3	*Cheiracanthium mildei*	Europe
Dysderidae (woodlouse hunters)	2	*Dysdera crocata*	Pacific Europe North America
Oonopidae (goblin spiders)	19	*Triaeris stenaspis* *Brignolia parumpunctata* *Ischnothyreus peltifer* *Opopaea concolor*	Africa Tropical Asia Tropical Asia Africa
Pholcidae (daddy-long-legs)	15	*Pholcus phalangioides* *Micropholcus fauroti* *Artema atlanta* *Smeringopus pallidus* *Spermophora senoculata*	Temperate Asia Temperate Asia Africa Africa Temperate Asia
Salticidae (jumping spiders)	34	*Plexippus paykulli* *Hasarius adansoni* *Menemerus bivittatus*	Africa Africa Africa
Scytodidae (spitting spiders)	8	*Scytodes thoracica*	Europe

Oecobiidae (disk web spiders)	9	*Oecobius navus*	Africa
Sicariidae (six-eyed spiders)	1	*Loxosceles rufescens*	North America Europe Australia Asia
Sparassidae (giant crab spiders)	3	*Heteropoda venatoria*	Tropical Asia
Theridiidae (cobweb or combfooted spiders)	47	*Parasteatoda tepidariorum* *Steatoda grossa* *Steatoda triangulosa* *Latrodectus geometricus*	South America Europe Europe Africa

Table 2.12. Top 10 most widespread invasive alien arachnids worldwide

The number of regions where the species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien species rather than their impacts which is covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	No. of regions	Species	No. of regions
***Raoiella indica* (red palm mite)**	7	*Steatoda nobilis* (false widow spider)	2
***Opilio canestrinii* (harvestman)**	3	*Tetranychus urticae* (two-spotted spider mite)	2
***Varroa destructor* (Varroa mite)**	3	*Aceria litchii* (litchi gall mite)	1
***Latrodectus geometricus* (brown widow spider)**	2	*Aceria tristriata* (walnut leaf gall mite)	1
***Mermessus trilobatus* (trilobate dwarf weaver)**	2	*Aculops lycopersici* (tomato russet mite)	1

2.3.1.8. Molluscs

Trends

Overall, molluscs have mostly been introduced unintentionally with numbers of introductions starting to increase at the end of 1800s (**Figure 2.14**). Similar to crustaceans, marine species introductions started when transoceanic voyages began around 1500 but were rarely documented (Carlton, 1999b). During the second half of the twentieth century, increases in shipping, aquaculture, and the aquarium trade facilitated the introductions of both marine and freshwater molluscs (Carlton, 1999a; Cianfanelli et al., 2016; Cowie, 2005; Darrigran et al., 2020; De Silva, 2012; X. Guo, 2009; Katsanevakis et al., 2013; Ojaveer et al., 2018; R. Sousa et al., 2014). A similar pattern is observed for terrestrial molluscs; they are almost exclusively moved as contaminants through agriculture and horticulture and their introductions began in ancient times (Herbert, 2010). Since 1600, European colonists have introduced many species to new areas (Herbert, 2010). With the increasing trade, introductions rates grew from the 1950s onward (Cowie, 2005; Herbert, 2010; Hutchinson et al., 2014).

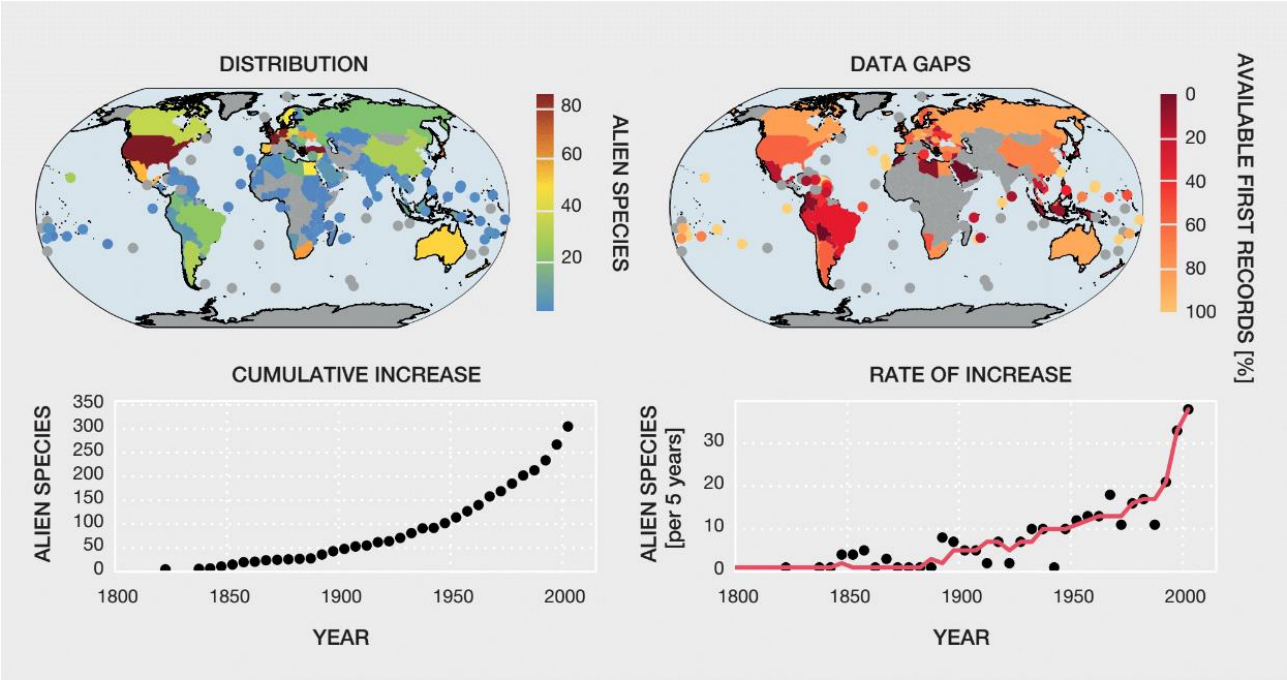

Figure 2.14. Status, trends, and data gaps for established alien molluscs. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (**section 2.1.4** for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. The trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (**section 2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at **https://doi.org/10.5281/zenodo.7615582**

Status

Established alien molluscs have been reported from all over the world (Capinha et al., 2015; R. Sousa et al., 2009). However, despite their status as widespread alien species and extensive work by malacologists in terrestrial and marine ecosystems (**Figure 2.14**) their distribution and spread has received comparatively little attention except for species such as *Dreissena* spp. (zebra and quagga mussels), *Corbicula fluminea* (Asian clam), and *Magallana gigas* (Pacific oyster) (Dölle & Kurzmann, 2020; Orlova et al., 2005; Ruesink et al., 2005; A. Sousa et al., 2009; Strayer et al., 2019). For bivalves, R. Sousa et al. (2009) listed examples of 35 established alien species in marine and freshwater systems of all continents, 24 of which have sufficient information about distribution or effects reported. However, the number of established alien bivalves is likely much higher than reported. Recently, *Mytilus* cf. *platensis* (mussel) was discovered in Antarctic waters (Cárdenas et al., 2020), further demonstrating that molluscs are transported in intercontinental transfers. Invasive bivalves often occur at very high densities becoming a major proportion of the benthic fauna (e.g., *Arcuatula senhousia* (Asian date mussel; Crooks & Khim, 1999), *Mytilus galloprovincialis* (Mediterranean mussel; Branch & Steffani, 2004), *Limnoperna fortunei* (golden mussel; Boltovskoy et al., 2006), *Perna viridis* (Asian green mussel; Rajagopal et al., 2006), and *Ensis leei* (American jack-knife clam; Raybaud et al., 2015)).

Marine bivalves (oysters, mussels, clams) have long been widely introduced for cultivation and harvesting in many regions of the world. Some were introduced to replace depleted or diseased

stocks of commercially valuable indigenous species, for example, *Magallana gigas* (Pacific oyster) and *Ruditapes philippinarum* (Japanese carpet shell) in Europe to diversify local marine farming, and *Mytilus edulis* (common blue mussel) in Canada and China (Tang et al., 2002). These alien species cause negative impacts in their introduced habitats by forming reefs on hard and soft bottoms and effecting large structural changes in littoral communities (**Chapter 4**, **section 4.3.2.3**).

Though of small size, some invasive alien molluscs attain high densities and cause remarkable impacts. *Littorina littorea* (common periwinkle) occurs at densities of up to 600 individuals per m² (Carlson et al., 2006), reduces algal canopies, and controls rocky intertidal community structure and species diversity (Bertness, 1984; Lubchenco, 1978; Petraitis, 1987; Yamada & Mansour, 1987). *Crepidula fornicata* (American slipper limpet) was introduced from the North American Atlantic coast to the Pacific coast and to Europe with *Crassostrea virginica* (eastern oyster). It forms dense conglomerations of live specimens, shells and pseudofaeces, transforming the physical and chemical composition of the sediment, which adversely affects the endobenthic community and reduces the area of flatfish habitat. When it fouls *Mytilus edulis* (common blue mussel), *Crepidula fornicata* increases mussel mortality by four to eight times, but also reduces mussel predation by *Asterias rubens* (common starfish; Blanchard, 2009; Kostecki et al., 2011; Thieltges, 2005a, 2005b). The easternmost Mediterranean is the region with the highest reported number of marine alien molluscs (over 160 species along 180 kms of Israeli and Palestine coast alone), most introduced through the Suez Canal (Galil et al., 2021b).

Alien snails and slugs have become established in most parts of the world, including on many islands. For example, 38 alien terrestrial snails and slugs are established in Hawaii (Cowie et al., 2008). Cowie et al. (2009) listed 46 species spanning 18 families for priority quarantine from the United States. *Lissachatina fulica* (giant African land snail) is one of the largest land snails in the world, reaching up to 19 cm in length, and is recognized as one of the world's most damaging invasive alien species because of its omnivorous nature and because it is a vector of at least two human diseases (W. M. Meyer et al., 2008; **Chapter 4**, **section 4.5.1.3**). *Euglandina rosea* (rosy predator snail) was originally introduced to control *Lissachatina fulica*. Not only did it fail to control it, but *Euglandina rosea* caused the extinction of many endemic snails on the islands of Hawaii, Tahiti, Moorea, and other Pacific islands (Davis-Berg, 2012; **Chapter 4**, **section 4.3.1**). Other widespread alien species include *Pomacea canaliculata* (golden apple snail; Q.-Q. Yang et al., 2018), *Arion ater* (european black slug; Zemanova et al., 2018), *Cepaea nemoralis* (grove snail), *Cornu aspersum* (common garden snail), *Limax maximus* (leopard slug), *Cernuella virgata* (vineyard snail), *Theba pisana* (white garden snail) and *Arion vulgaris* (Spanish slug). **Table 2.13** lists the 10 most widespread alien mollusc species invasive in most regions.

Table 2.13. Top 10 most widespread invasive alien mollusc species worldwide

The number of regions where the species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien mollusc species rather than their impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	**No. of regions**	**Species**	**No. of regions**
***Lissachatina fulica* (giant African land snail)**	31	*Pomacea canaliculata* (golden apple snail)	13
***Corbicula fluminea* (Asian clam)**	22	*Arcuatula senhousia* (Asian date mussel)	10
***Dreissena polymorpha* (zebra mussel)**	20	*Melanoides tuberculata* (red-rimmed melania)	10

***Magallana gigas* (Pacific oyster)**	15	*Corbicula fluminalis* (Asian clam)	9
***Potamopyrgus antipodarum* (New Zealand mudsnail)**	15	*Dreissena rostriformis bugensis* (quagga mussel)	9

2.3.1.9. Crustaceans

Trends

Unintentional introductions of marine crustaceans probably began in the 1500s when transoceanic voyages were first undertaken (Carlton, 2011), but no data are available. The first records of alien crustaceans were reported between the 1800s and the beginning of 1900s (Carlton, 2011; **Figure 2.15**). Like those of other alien marine species, crustacean introductions have risen in recent decades due to increased shipping, fisheries, aquaculture, and aquarium trade (Fernández de Alaiza García Madrigal et al., 2018; Hänfling et al., 2011; Katsanevakis et al., 2013; Ojaveer et al., 2018). For example, the Suez Canal allowed the entry of alien crustaceans into the Mediterranean Sea for the entire twentieth century with an increase from 1990 facilitated by climate warming (Galil, 2011). The unintentional introduction of freshwater species started with global shipping and the construction of artificial canals (e.g., in Central and Western Europe), increasing after the 1950s. Overall, crustaceans were one of the most frequently introduced groups in recent decades in the Baltic Sea, California Bay, and the Laurentian Great Lakes (Hänfling et al., 2011). On the other hand, crayfish have been intentionally introduced as a food source since the end of 1800s (Hänfling et al., 2011), but global increases of crayfish production starting in the 1970s boosted introductions (Haubrock et al., 2021; Lodge et al., 2012).

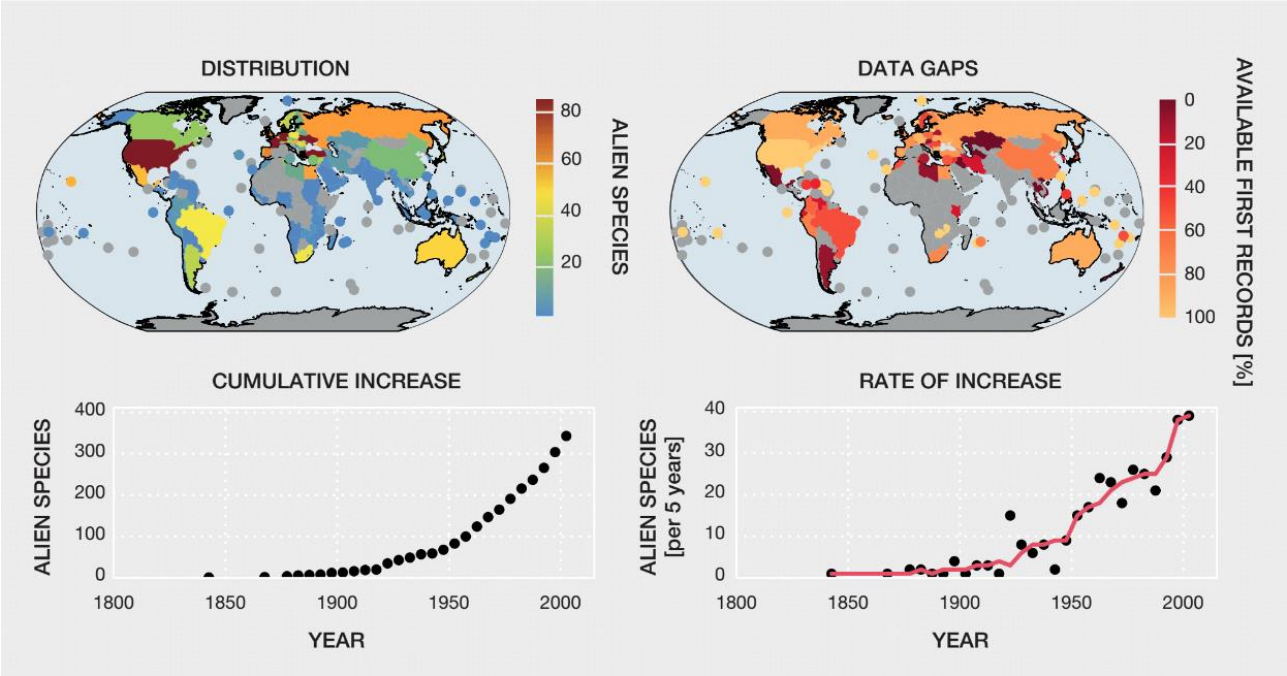

Figure 2.15. Status, trends, and data gaps for established alien crustaceans. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (section 2.1.4 for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. The trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend line is calculated as running median (section 2.1.4 for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources.

A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Crustaceans are frequently found among lists of marine and freshwater alien species (Galil et al., 2011; Hänfling et al., 2011; Simões et al., 2021). As an example, the Mediterranean, North East Atlantic, Black and Baltic Seas host some of the highest species numbers, with 1,411 established alien species reported (Tsiamis et al., 2018), a noteworthy proportion of which includes crustaceans (Tsiamis et al., 2020). Owing to human activities, many marine crustacean species have achieved global distributions (e.g., barnacles *Balanus glandula* (Kerckhof et al., 2018), *Amphibalanus improvisus* (bay barnacle), and *Amphibalanus eburneus* (ivory barnacle); isopods *Synidotea laevidorsalis* (J. W. Chapman & Carlton, 1991) and *Ianiropsis serricaudis*; amphipod *Caprella mutica* (Japanese skeleton shrimp); shrimp *Palaemon macrodactylus* (oriental shrimp); additional shrimp and many crab species; many copepods and mysids; and several more).

Hemigrapsus sanguineus (Asian shore crab) is now the dominant crab in rocky intertidal habitats along much of the north-eastern coast of the United States and the European Atlantic coast where it has been introduced and displaces resident crab species (Blakeslee et al., 2017; Epifanio, 2013). The literature on the Asian shore crab is limited in comparison to that of better-known global marine invasive established crabs like *Carcinus maenas* (European shore crab), *Carcinus aestuarii* (Mediterranean green crab) (Cosham et al., 2016; Leignel et al., 2014), and *Eriocheir sinensis* (Chinese mitten crab; Dittel & Epifanio, 2009). **Table 2.14** lists the 10 most widespread invasive alien crustacean species and the number of regions each has invaded.

Crustaceans also comprise major proportions of alien animals established in large freshwater ecosystems; their rate of discovery, along with that of other freshwater invertebrates, is increasing in these habitats (Ricciardi, 2015). According to Gherardi (2010), 28 crayfish species have been introduced into a new biogeographic region and/or translocated within their native biogeographic region. In Europe, most crayfish species are alien (at least 10 alien, five native), with significantly higher abundances and severe impacts caused by alien crayfish, especially the transmission of crayfish plague, a disease lethal to native species (Kouba et al., 2014; **Chapter 4**, **section 4.3.2.2**). There is increasing recognition of their severe impacts, notably the displacement of native species (Gherardi, Aquiloni, et al., 2011; South et al., 2020). In Africa, five out of nine introduced crayfish species established populations in at least six countries, causing substantial ecological and economic damage (Madzivanzira et al., 2021). Genetic divergence between European and North American lineages of freshwater cladocerans suggests that the current rate of invasion by European species in North America is ca. 50,000 times higher than prehistoric levels (Hebert & Cristescu, 2002). Invasions of the Laurentian Great Lakes (**Box 2.11**) by two cladocerans, *Cercopagis pengoi* (fishhook waterflea), and *Bythotrephes longimanus* (spiny waterflea), have caused concern for freshwater biodiversity and regional fisheries (Pichlová-Ptáčníková & Vanderploeg, 2009). *Dikerogammarus villosus* (killer shrimp) is a physiologically tolerant and adaptable amphipod of Ponto-Caspian origin that has colonized most of the major European inland waterways in only two decades, replacing many local amphipod species. Its continued range expansion, as well as its potential to reach freshwaters of other continents (particularly North America and its Great Lakes), is a major conservation concern (Rewicz et al., 2014). *Hemimysis anomala* (bloody-red shrimp) was one of several Ponto-Caspian species to invade the Great Lakes in recent decades through transoceanic shipping (Audzijonyte et al., 2007).

Table 2.14. Top 10 most widespread invasive alien crustacean species worldwide

The number of regions where the species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien

crustacean species rather than their impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	No. of regions	Species	No. of regions
***Pacifastacus leniusculus* (American signal crayfish)**	19	*Dikerogammarus villosus* (killer shrimp)	12
***Procambarus clarkii* (red swamp crawfish)**	19	*Cherax quadricarinatus* (redclaw crayfish)	11
***Amphibalanus improvisus* (bay barnacle)**	17	*Chelicorophium curvispinum* (Caspian mud shrimp)	10
***Faxonius limosus* (spiny-cheek crayfish)**	14	*Cercopagis pengoi* (fishhook waterflea)	8
***Eriocheir sinensis* (Chinese mitten crab)**	12	*Macrobrachium rosenbergii* (giant freshwater prawn)	7

2.3.1.10. Other invertebrates

Other invertebrates cover those invertebrate species that are not addressed in previous sections and include the phyla Acanthocephala, Annelida, Brachiopoda, Bryozoa, Chaetognatha, Cnidaria, Ctenophora, Echinodermata, Kamptozoa, Nematoda, Nemertea, Onychophora, Phoronida, Platyhelminthes, Porifera, Rotifera, Sipuncula and Xenacoelomorpha.

Trends

There is a paucity of data on molluscs, and crustaceans, but there is nothing to suggest that the trends for these animals differ from the better documented groups. In fact, data on the trends in both cumulative numbers and number of established alien species per five-year intervals show that animals other than the aforementioned vertebrates and invertebrates follow the same dramatic global increases since ca. 1850 (**Figure 2.16**). For example, jellyfish populations appear to be increasing post-1950 in coastal ecosystems worldwide, mostly due to increasing populations of invasive alien species (Brotz et al., 2012; importantly, note that Brotz et al. (2012) defined "jellyfish" as including three separate phyla of marine invertebrates - Cnidaria, Ctenophora, and Chordata). The increase has accelerated in recent decades and climate change is likely playing a role in facilitating increased survival and growth, and access to previously unfavourable waters. The depletion of predators and food competitors due to overfishing was also important (A. J. Richardson et al., 2009). Notably, several comb jelly species (ctenophores) often survive ballast-water exchange, and their populations have been found to expand in over-fished areas that provide favorable conditions (Daskalov et al., 2007). The invasion of the Black, Caspian, Baltic, and North Seas by the comb jelly *Mnemiopsis leidyi* (sea walnut) in the recent decades is a good illustration (Boersma et al., 2007; Daskalov & Mamedov, 2007; Haslob et al., 2007; Zaitsev, 1992). The increase of invasive alien jellyfish and comb jellies is predicted to continue accelerating (A. J. Richardson et al., 2009). Other marine species, such as *Anemonia alicemartinae* (sea anemone), are considered invasive along the coast of Chile, and historical records show a rapid expansion towards the south, extending its distribution (Castilla et al., 2005; Castilla & Neill, 2009; Häussermann & Försterra, 2001).

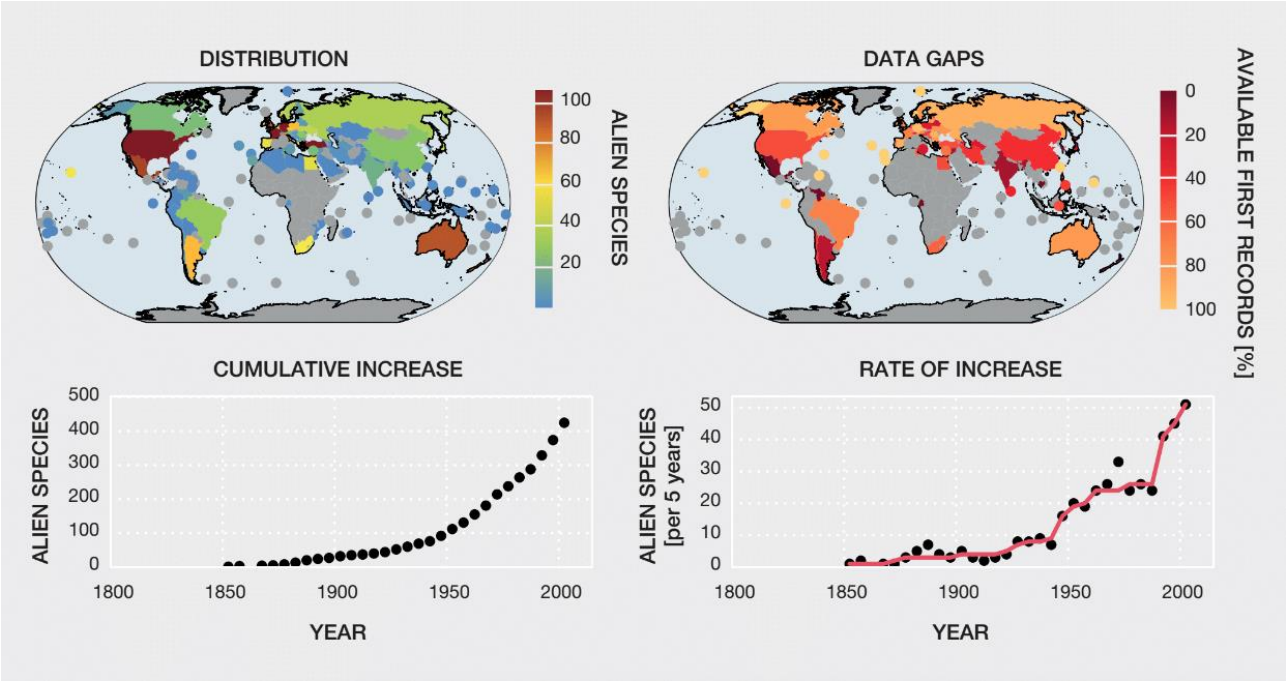

Figure 2.16. Status, trends and data gaps for other established alien invertebrates. Other established alien invertebrates refer to animal groups, which are not covered in the previous sections. The names of the taxonomic groups are listed at the beginning of **section 2.3.1.10**. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (**section 2.1.4** for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (**section 2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Comprehensive studies for invertebrates, other than those reported above, are often lacking and detailed knowledge is usually available for only a few species. *Asterias amurensis* (northern Pacific seastar) is considered one of the most serious marine pests in Australia (MPSC, 2018). The same concern arises for *Centrostephanus rodgersii* (long-spined sea urchin). Its invasion from mainland Australia to Tasmania has already caused ecosystem shifts from kelp-dominated to a macroalgal-free habitat resulting in localized losses of about 150 taxa that associate with seaweed beds (Ling et al., 2009). Among ctenophores, a prominent representative is the previously mentioned *Mnemiopsis leidyi* (sea walnut), first introduced from the North American east coast to the Black Sea in ship ballast water. The species subsequently spread throughout the Ponto-Caspian basin and the Mediterranean Sea, ultimately spreading across most European seas due to a climate-driven range expansion rather than a human-mediated introduction (Shiganova et al., 2019).

Many earthworm species can be regarded as "ecosystem engineers," that is they play a pronounced role in the creation, modification and maintenance of the upper horizons of the soil habit (Eijsackers, 2011; C. G. Jones et al., 1994; Ponge, 2021). The potential for modifying the soil environment means that earthworms can have a disproportionate impact on the communities that they invade (Hendrix et al., 2008). This is especially true in circumstances where earthworms

invade soils that previously had an absent or impoverished earthworm fauna (Frelich et al., 2019). Globally, more than 100 alien earthworm species are documented (Hendrix, 2006) but have mostly been neglected until very recently. For example, earthworm invasions in North America date back to the first European settlers, but because they live underground, they have remained mostly unnoticed (Migge-Kleian et al., 2006). Ongoing invasions of European earthworms into the Upper Midwest of the United States are relatively well documented (Hale et al., 2005) compared to the invasion in the Northeast (Stoscheck et al., 2012; Suárez et al., 2006). Alien earthworms can often be found spreading into habitats where few or no native earthworms exist, such as in North America which has been depauperate in native earthworms since the last glaciation (McCay & Scull, 2019). Similar patterns are believed to exist in the taiga region in Russia and the coniferous forests of Scandinavia (Hendrix, 2006). The earthworm fauna of the North American northeast now includes a few native species (Csuzdi et al., 2017), many alien species from Europe, and a rapidly rising number of species from Asia (Addison, 2009; McCay & Scull, 2019). The tropical earthworm *Pontoscolex corethrurus*, originally native to Guyana, was introduced to tropical and sub-tropical regions worldwide (S. Taheri et al., 2018). *Platydemus manokwari* (New Guinea flatworm) was both unintentionally and deliberately introduced into the soils of many countries and islands, where it leads gregarious attacks on large earthworms and land snails (Sugiura, 2010; Sugiura & Yamaura, 2009). Another flatworm, *Obama nungara* from South America, has been introduced to France (Justine et al., 2020). *Arthurdendyus triangulatus* (New Zealand flatworm) can now be found in Great Britain where it causes declines in native earthworm populations (Murchie & Gordon, 2013).

There is a growing recognition of the influence of alien earthworms in tropical environments as well (Marichal et al., 2012; Ortíz-Ceballos et al., 2019; Potapov et al., 2021; S. Taheri et al., 2018). Earthworm communities in tropical agricultural environments often consist of both native and invasive alien species; however, it is not always clear what role these species are playing, though, without doubt, deforestation, the spread of plantations, landscaping and an expansion of human activity may serve as drivers that facilitate further invasion (Potapov et al., 2021).

Along the south-eastern Pacific coast, there are records for six introduced species of polychaete worms from the families Spionidae and Sabellidae (Fuentes et al., 2020; Moreno et al., 2006). The species *Polydora rickettsi*, *Polydora hoplura* and *Terebrasabella heterouncinata* were accidentally introduced. There is no information regarding the type of introduction for *Boccardia tricuspa*, *Polydora bioccipitalis* and *Dipolydora giardi* (Fuentes et al., 2020). All of them compete with the native species. These introductions also cause negative economic impacts in the aquaculture industry by boring and infesting the shells of cultured molluscs (Fuentes et al., 2020; Moreno et al., 2006; **Chapter 4**, **Box 4.13**).

2.3.1.11. Data and knowledge gaps

Global analyses on invasion trends and status for animals are limited to some taxonomic groups, such as mammals, birds, reptiles, amphibians, fish, land snails, spiders, crustaceans and ants. Many case studies exist on species of other groups, but they provide substantially less information on general patterns.

Data and knowledge gaps are pervasive across all taxonomic groups and geographical levels (**Figure 2.6**; Pyšek et al., 2008; Troudet et al., 2017). Charismatic species such as birds and mammals tend to be more studied while other taxa, such as herpetofauna and invertebrates, have weaker sampling efforts and hence more data gaps (Pyšek et al., 2008; Rocha-Ortega et al., 2021; Troudet et al., 2017). However, even the most intensively studied taxa may not be fully documented at the global scale resulting in geographic biases mainly driven by economic development (Dawson et al., 2017) and linguistic barriers (Angulo et al., 2021; Nuñez & Amano, 2021). The data gaps comprising both taxonomic groups and geographical regions in the marine realm are particularly

apparent. Unlike terrestrial and freshwater alien species, marine alien species are mostly unintentionally introduced, and most records are either confined to economically impactful species, or to (relatively) large-sized sessile taxa inhabiting the intertidal or the shallow shelf. Even for these taxa, surveys have not been conducted along region-wide coastlines, leaving most alien taxa undetected and unrecognized. This presents an enormous challenge for understanding the dynamics of these biological invasions and prioritizing conservation and research aims for marine ecosystems (Ojaveer et al., 2015, 2018).

Comprehensive analyses of data and knowledge gaps of alien species occurrences are largely lacking on a global scale. The few global systematic reviews of alien species distributions available for well-studied taxonomic groups such as mammals (Biancolini et al., 2021), birds (E. E. Dyer, Cassey, et al., 2017), reptiles and amphibians (Capinha et al., 2017) indicate large geographic areas of incomplete information. For example, global systematic reviews of studies of first record data for alien amphibians and reptiles (N. J. van Wilgen et al., 2018; **Figures 2.10** and **2.11**) using model-based estimates of the number of alien turtles expected to be introduced but not detected worldwide (García-Díaz et al., 2015), showed consistent spatial gaps. Alien reptiles and amphibians have been understudied in Africa and parts of Asia, whereas the knowledge of alien amphibians and reptiles in Meso- and South America varies by country. These spatial patterns broadly mirror those of native reptiles and amphibians assessed as data-deficient in global International Union for Conservation of Nature (IUCN) Red List of threatened species assessments (Böhm et al., 2013; Stuart et al., 2008) and are very similar for other taxonomic groups.

In some cases, even though large regions are indicated as invaded due to country-level reporting, it is likely that only certain areas of these countries are actually invaded. This coarse scale reporting may cause distorted understanding of global distribution maps of these species by assigning very large territories to invasions while in fact, only smaller areas might be concerned. When numbers of invasive alien species are compiled, large countries are more likely to be tallied as containing species, even if their distributions are not greater than in smaller countries, thus contributing to this bias. Also, species introduced to new parts of a country where they did not previously exist are often not reported as being alien, and therefore, total numbers of alien species are frequently underestimated.

Data documenting invertebrate invasions are grossly incomplete. Earthworms are understudied compared to the impact they have on invaded ecosystems (Hendrix, 2006; Porco et al., 2013). Many invertebrates are small and inconspicuous, and so large numbers of alien invertebrates remain undetected. For example, many Hymenoptera parasitoids have likely invaded regions without being detected likely due to a lack of available expertise and monitoring. The Asian parasitic wasp species *Gryon japonicum* (samurai wasp) was being evaluated for introduction as a biological control agent of *Halyomorpha halys* (brown marmorated stink bug) in North America when researchers discovered that it was already present (Talamas et al., 2015). Addressing this problem not only requires increased survey effort, but also requires increased taxonomic research, since many insect species remain undescribed.

Research efforts are also driven by the actual, perceived, or projected impacts of invasive alien species, with highest-impact species being the most studied (e.g., bivalves, a small number of ants, a few other insects, some crustaceans, most vertebrates), while those causing less conspicuous damage are sometimes neglected (Pyšek et al., 2008). For example, of the 19 highly invasive ant species, only two are extensively studied (over 350 studies each in Web of Science), three are much less covered, and the remaining species are almost entirely ignored (more than 3 per cent of all studies for the 14 other species cumulatively; Bertelsmeier et al., 2016). Such disparities reflect presumed impacts and can potentially bias studies towards species with high expected impacts, but they also reflect the low number of biological invasion researchers and managers relative to the number of insect invasions.

Other factors contributing to data and knowledge gaps include taxonomic uncertainties, inadequate historical records, lack of data mobilization (i.e., making data available and accessible), sharing, and insufficiently applied expertise. Many ecosystems – especially freshwater and marine systems – harbour species that cannot be categorized as either alien or native with any high degree of certainty. In other cases, alien species are wrongly and erroneously assumed to be native and to have a natural cosmopolitan distribution (Carlton, 2009; Jarić et al., 2019). The problem is most severe for small-bodied invertebrates (Marchini & Cardeccia, 2017; Ruiz & Carlton, 2003). Freshwater examples include bryozoans and rotifers, which are ubiquitous in lakes and rivers and have resting stages that are common and abundant in the ballast water of some transoceanic ships (Kipp et al., 2010), but are rarely reported as alien species even in highly invaded aquatic systems (Pociecha et al., 2016; Ricciardi, 2015).

In addition to information on the occurrence of alien populations, the dates of first introduction are unknown for most taxa except for avian and mammalian species (Biancolini et al., 2021; E. E. Dyer, Redding, et al., 2017). In general, more of this temporal information exists for Europe, especially for mammals and birds, while large gaps are found in Central Africa and South Asia. However, in most cases, the proportion of species with available temporal information is far below 50 per cent (Seebens et al., 2020), often including well-studied regions like North America and Europe. Furthermore, there is a severe gap in temporal information for invertebrates all over the world.

More work to address the current knowledge gaps remains to be done. In particular, further genetic research including environmental deoxyribonucleic acid (DNA; Herder et al., 2014; Hunter et al., 2015; Tingley et al., 2019) will contribute to resolving the alien or native status of some species and to uncovering cryptic and unrecognized introductions (Cogălniceanu et al., 2014; Silva-Rocha et al., 2012; Telford et al., 2019).

2.3.2. Plants

This section reports on the temporal trends and status of the distribution of alien and invasive alien plant species for vascular plants (**section 2.3.2.1**), aquatic plants (**section 2.3.2.2**), algae (**section 2.3.2.3**) and bryophytes (**section 2.3.2.4**) as well as data and knowledge gaps (**section 2.3.2.5**).

2.3.2.1. Vascular plants

Trends

The total number of alien plant species established outside of their native ranges worldwide has increased continuously for centuries (**Figure 2.17**), and first records of alien plants dating back more than one thousand years exist from all over the world (van Kleunen et al., 2019; Wijesundara, 2010). As with many other taxonomic groups, the rate of accumulation for plants rose dramatically in the second half of the nineteenth century, tapering off in the early twentieth century, but increasing steeply after ca. 1970. Indeed, 28 per cent of all established plant records worldwide were recorded for the first time after 1970 (**Figure 2.17**).

The number of alien plant species introduced is particularly important because plant introductions (whether intentional or unintentional) are a pathway for other invasive alien species introductions such as forest pests and pathogens, microbes, and other hitchhikers (Hulme et al., 2008). The historical flow of alien plant species among continents shows that Europe and temperate Asia are the major donors of established alien plant species to other parts of the world (Drake et al., 1989; van Kleunen et al., 2015). The number of species native to Europe that have been established elsewhere is almost three times higher than expected (van Kleunen et al., 2015). North America is also over-represented, with 57 per cent more species donated than expected based on native

continental richness. In contrast, the continents in the Southern Hemisphere are all under-represented as donors of alien species. This suggests that, at least for plants, the "Old World versus New World" dichotomy (a classical concept in biological invasions suggesting that "Old World" biota were more likely to invade other parts of the globe due to traits they developed in close association with humans in their native ranges; Di Castri, 1989) needs to be replaced by a Northern Hemisphere versus Southern Hemisphere dichotomy for the donor continents of established alien plants (van Kleunen et al., 2015).

While North America has accumulated the greatest number of established alien species, the Pacific islands show the fastest increase in species numbers with respect to land area suggesting that Pacific islands have the highest vulnerability to invasions of all areas globally. Oceanic islands harbour more established alien plant species than similarly sized mainland regions, a phenomenon traditionally attributed to the niche space being unsaturated by native species or to a greater frequency of introductions (Moser et al., 2018; van Kleunen et al., 2015). Given the high concentration of endemic species on most oceanic islands, the large numbers of established alien species constitute a serious threat to global biodiversity (Fernández-Llamazares et al., 2021; Pyšek, Blackburn, et al., 2017; van Kleunen et al., 2015).

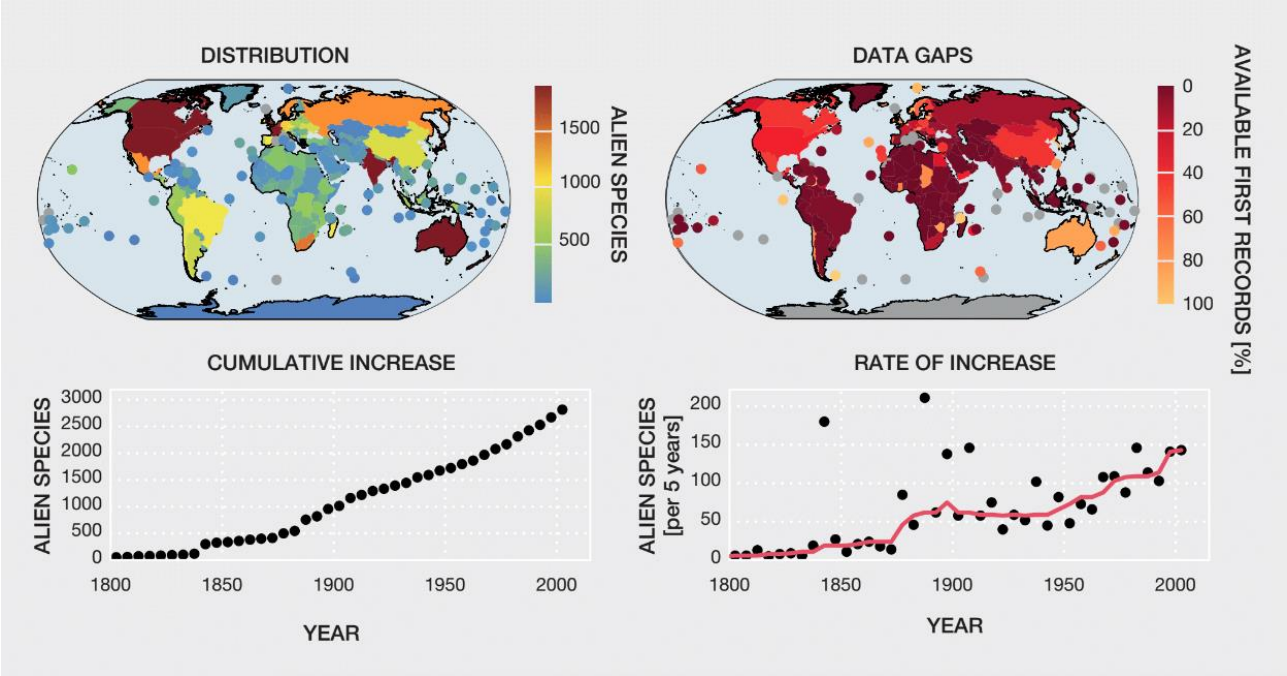

Figure 2.17. Status, trends, and data gaps for established alien vascular plants. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (section 2.1.4 for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of alien species per five years). Smoothed trend (line) is calculated as running median (section 2.1.4 for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582.

Status

Currently, the total number of established alien plant species (13,939 species; van Kleunen et al., 2019) indicates that at least 4 per cent of all known vascular plant species (337,137 species; The

Plant List, 2015) have become established outside their natural ranges because of human activity. In total, 12,345 established alien species are reported from mainland regions globally and 8,019 from islands (Pyšek, Pergl, et al., 2017).

The cool temperate forest and woodland regions have the highest richness of established alien plant species (6,586 species), followed by tropical (equatorial 4,690 species, and savanna 4,843 species), and warm temperate regions (4,649 species). In total, temperate regions harbour 9,036 established alien species relative to 6,774 for tropical zones, 3,280 in the Mediterranean regions, 3,057 in subtropical regions, and 321 in Arctic regions. When the total number of established alien species is standardized to the area of each region by comparing species accumulation rates with area, it appears that colder temperate and Mediterranean regions are more heavily colonized by alien species while more arid regions have fewer (**Figure 2.17**; Pyšek, Pergl, et al., 2017).

Hotspots of relative alien species richness (i.e., the per cent of established alien species in the total regional flora) appear on both the western and eastern coasts of North America, north-western Europe, South Africa, south-eastern Australia, New Zealand, and India. South Africa, India, California (United States), Cuba, Florida (United States), Queensland (Australia) and Japan have the highest absolute values of established alien species (Essl et al., 2019; Pyšek, Pergl, et al., 2017). The mainland regions with the highest numbers of established alien species include several Australian states (New South Wales is highest in established alien richness on this continent) and several North American regions such as California, which has 1,753 established alien plant species. High levels of island colonization by established alien plants are concentrated in the Pacific region, but also occur on individual islands across all oceans. About one quarter (26 per cent) of the islands investigated by Essl et al. (2019) now have more established alien species than native species. England, Japan, New Zealand, and the Hawaiian archipelago harbour most established alien plants among islands or island groups (Pyšek, Pergl, et al., 2017). Numbers of established alien species are closely correlated with those of native species and also with those of invasive alien species. There is also a faster increase in the numbers of established alien species with area on islands than in mainland regions, indicating a greater vulnerability of islands to alien species establishment (Essl et al., 2019; Pyšek, Pergl, et al., 2017).

Among vascular plants, the introduction of alien ferns is certainly less investigated and only one global assessment for alien ferns exists (E. J. Jones et al., 2019). This study lists 157 alien ferns which are found in all climatic zones except the Arctic and Antarctic and on all continents. High numbers of alien ferns were reported for New Zealand, Hawaii, India and Europe.

In terms of plant families, rankings by absolute numbers of established alien species reveal that Asteraceae (1,343 species), Poaceae (1,267) and Fabaceae (1,189) contribute most to the global established alien flora. Comparing the number of established alien species in a family to its total global richness reveals that some of the large species-rich families are over-represented among established alien species (e.g., Poaceae, Fabaceae, Rosaceae, Amaranthaceae, Pinaceae), some under-represented (e.g., Euphorbiaceae, Rubiaceae), whereas Asteraceae, which has the highest richness of established alien species, reaches an expected value based on its global species richness. A significant phylogenetic signal indicates that some plant families have a higher potential for species to establish (Pyšek, Pergl, et al., 2017). *Solanum* (112 species), *Euphorbia* (108) and *Carex* (106) are the richest genera in terms of established alien species. Some families are disproportionately over-represented by alien species on islands (i.e., Arecaceae, Araceae, Acanthaceae, Amaryllidaceae, Asparagaceae, Convolvulaceae, Rubiaceae, Malvaceae), but significantly fewer families are over-represented on mainlands (e.g., Brassicaceae, Caryophyllaceae, Boraginaceae). On islands, the genera *Cotoneaster*, *Juncus*, *Eucalyptus*, *Salix*, *Hypericum*, *Geranium*, and *Persicaria* are over-represented, while on the mainland *Atriplex*, *Opuntia* (pricklypear), *Oenothera*, *Artemisia*, *Vicia*, *Galium*, and *Rosa* are relatively richer in established alien species (Pyšek, Pergl, et al., 2017).

Table 2.15. Top 10 most widespread invasive alien vascular plant species worldwide

The number of regions where the species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien vascular plant species rather than their impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	No. of regions	Species	No. of regions
***Pontederia crassipes* (water hyacinth)**	74	*Robinia pseudoacacia* (black locust)	45
***Lantana camara* (lantana)**	69	*Chromolaena odorata* (Siam weed)	43
***Leucaena leucocephala* (leucaena)**	55	*Pistia stratiotes* (water lettuce)	41
***Ricinus communis* (castor bean)**	47	*Erigeron canadensis* (Canadian fleabane)	38
***Ailanthus altissima* (tree-of-heaven)**	46	*Cyperus rotundus* (purple nutsedge)	37

The 10 most widely distributed established alien plants globally occur in at least 35 per cent of the world's regions. Other species such as *Sonchus oleraceus* (common sowthistle) occur in 48 per cent of the regions corresponding to 42 per cent of the globe. Additional widely distributed established alien species are *Oxalis corniculata* (creeping woodsorrel), *Portulaca oleracea* (purslane), *Eleusine indica* (goose grass), *Chenopodium album* (fat hen), *Capsella bursa-pastoris* (shepherd's purse), *Stellaria media* (common chickweed), *Bidens pilosa* (blackjack), *Datura stramonium* (jimsonweed), and *Echinochloa crus-galli* (barnyard grass). However, the ranking for invasive alien species differs among global databases because the data differ depending on the source used. The GloNAF database highlights *Lantana camara* (lantana,120/349 regions for which data on invasive status are known), *Calotropis procera* (apple of sodom, 118), *Pontederia crassipes* (water hyacinth, 113), *Sonchus oleraceus* (108) and *Leucaena leucocephala* (leucaena, 103) as the most distributed invasive alien species (Pyšek, Pergl, et al., 2017), while GRIIS (Pagad et al., 2022) provides a different ranking (**Table 2.15**).

Box 2.2. Cacti, grasses and woody species: A global assessment of trends and status of alien and invasive alien species

Cacti (Cactaceae, about 1,922 species), grasses (Poaceae, about 11,000 species) and woody species are among the most studied species from a plant invasion perspective.

Cacti, native to the Americas, were among the first plants brought back by European explorers from the Americas in the fifteenth century. Most cacti (about 1,600 species, 81 per cent of the family) have been introduced outside their native ranges via the horticultural trade, especially recently due to higher volumes of e-commerce (**Glossary**; Novoa et al., 2017), rapidly increasing the number of established alien cactus species (**Figure 2.18**). However, only 3 per cent of species in Cactaceae (57 species) are currently considered as invasive alien species (Novoa et al., 2015), with *Opuntia ficus-indica* (prickly pear) being the most widespread (**Figure 2.19**). Although countries such as France, India or the United States support many established alien cacti (**Figure 2.20**), there are three main hotspots for invasive alien cacti globally: South Africa (35 species recorded), Australia (26 species) and Spain (24 species). Most invasive alien cacti are native to Argentina, Mexico, and North America, which are roughly bioclimatically similar to the invaded regions. Other large regions, such as China, North- and South-East Asia, and Central Africa that are not

intensively invaded by cacti have suitable climates for invasive cacti and therefore are at risk of future invasions (**Glossary**; Novoa et al., 2015).

Grasses have been introduced outside their native ranges for horticulture, soil stabilization, as food and fodder, as biofuel, or as raw materials. Most remarkably, forage grasses have been a major focus of plant introduction programmes across large areas (Visser et al., 2016). Perhaps as a result of such large introduction events, the number of established alien grass species has been intermittently increasing since the nineteenth century (**Figure 2.18**). Currently, 1,226 alien grass species are reported as established globally (Pyšek, Pergl, et al., 2017). Regions with the highest numbers of established alien grasses are Indonesia, Hawaii, Madagascar, New Zealand, tropical Africa, tropical South America and the southern United States (**Figure 2.20**). Among all grasses, tall-statured grasses (defined as grass species that maintain a self-supporting height taller than or equal to 2 meters; 929 species) are 2–4 times more likely to establish than shorter grasses (Canavan et al., 2019). This is due in part to their rapid growth rates and capacity to accumulate biomass. Tropical Africa (especially islands in the Western Indian Ocean) is the main hotspot of established alien tall statured grasses, with this group accounting for 30 to 70 per cent of all established alien grasses. The Caribbean is another such hotspot (Canavan et al., 2019). Overall, 80.6 per cent of all tall statured grasses are woody bamboos, of which *Bambusa vulgaris* (common bamboo) is the most widespread species (**Figure 2.20**).

Many **woody species** (shrubs and trees) are among the most widespread and damaging invasive plants (D. M. Richardson & Rejmánek, 2011). While there is no precise data available on the number of established woody species, D.M. Richardson and Rejmánek (2013; 2011) compiled a global database of 751 invasive alien woody species, comprised of 434 trees and 317 shrubs in 90 plant families and 286 genera. These alien species were introduced outside of their native ranges through many pathways including horticulture (62 per cent of invasive woody species: 196 trees and 187 shrubs), forestry (13 per cent), food (10 per cent), and agroforestry (7 per cent). Regions with the largest numbers of woody invasive alien species are North America (212), Pacific Islands (208), Australia (203), Southern Africa (178), Europe (134), and Indian Ocean Islands (126). Taxa within the genera *Acacia* and *Pinus* (Pine) comprise a large portion of the woody invasive alien species globally. In particular, *Pinus* (comprising 111 tree and shrub species, only one of which has its natural range confined to the Northern Hemisphere) have been widely introduced and planted in many areas well outside their native range and are among the most widely used forestry species worldwide (D. M. Richardson et al., 1994). At least 30 *Pinus* species are known to be established alien species and 21 invasive alien species (D. M. Richardson, 2006). *Pinus contorta* (lodgepole pine) is one of the most invasive plantation trees (**Figure 2.19**). Native to northwest North America, it is established in Great Britain, Ireland, and Russia, and is an invasive alien species in Argentina, Australia, Chile, New Zealand, and Sweden (Langdon et al., 2010). *Pinus* invasions were first recorded in South Africa in 1855, in New Zealand in 1880 and in Australia in the 1950s (20-30 years after the first large plantations were established), and most research on *Pinus* invasions has been done in those countries (Simberloff et al., 2009). However, because of a recent increase in commercial *Pinus* plantations in South America (Argentina, Brazil, Chile, and Uruguay are the countries having the greatest area of planted *Pinus*), *Pinus* invasions are currently an emerging problem on the continent and are predicted to increase rapidly in the next few decades (D. M. Richardson et al., 2008). Acacias (about 1,350 species), especially Australian acacias (species within the genus *Acacia* that are native to Australia, about 1,012 species), have also been widely introduced outside their native ranges for centuries (D. M. Richardson et al., 2011). At least 386 Australian acacias have been introduced outside Australia, of which 71 are recorded as established alien species and 23 as invasive alien species. The extent of Australian acacia invasions is likely to increase in the future, given that climatic models have suggested that a third of the world's terrestrial surface is climatically suitable. For example, *Acacia dealbata* (acacia bernier; **Figure 2.19**) is currently recorded as an invasive alien species in seven countries (D. M. Richardson &

Rejmánek, 2011). Since it has been introduced widely outside of Australia, further accounts of its invasion are likely.

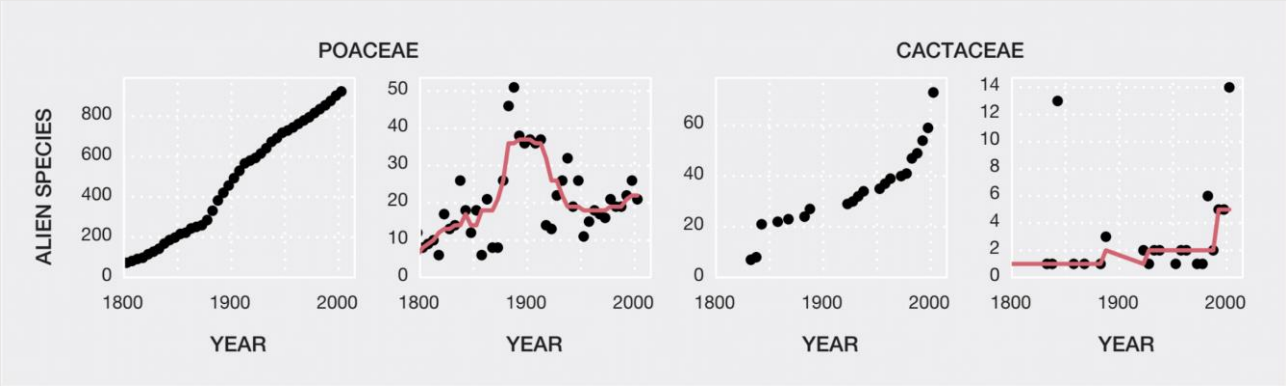

Figure 2.18. Trends in numbers of established alien species for Poaceae and Cactaceae. Cumulative numbers (left panels) and number of established alien species per five-year intervals (right panels). Numbers shown underestimate the true extent of alien species occurrences due to a lack of data. Smoothed trends (line) are calculated as running medians (**section 2.1.4** for further details about data sources and data processing). A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Figure 2.19. Examples of the most widespread invasive cacti, grasses and woody species. *Opuntia ficus-indica* (prickly pear; top left) is the most commercially important cactus and is recorded as invasive in 26 countries worldwide. *Bambusa vulgaris* (common bamboo; top right) is the most widely cultivated bamboo and recorded as invasive in 5 countries. *Pinus contorta* (lodgepole pine; bottom left) is one of the most invasive plantation trees and it is recorded as invasive in 5 countries.

Acacia dealbata (acacia bernier; bottom right) was introduced to many regions for multiple purposes and is now a widespread invasive alien species in 7 countries. Photo credit: Nicole Pankalla, Pixabay - under license CC BY 4.0 (top left) / Bishnu Sarangi, Pixabay - CC BY 4.0 (top right) / Walter Siegmund - CC BY 4.0 (bottom left) / Ulrike Leone, Pixabay - CC BY 4.0 (bottom right)

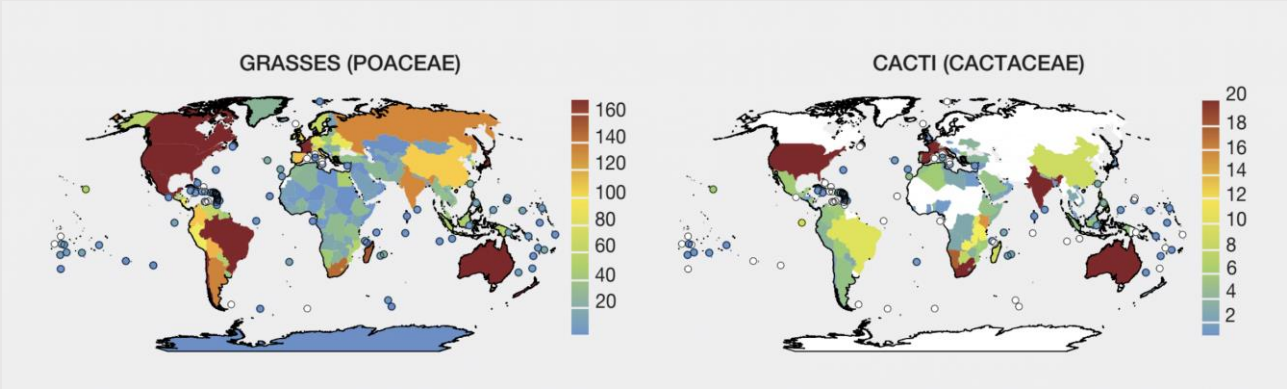

Figure 2.20. Numbers of established alien grasses and cacti worldwide. Colours indicate established alien species of the families Poaceae and Cactaceae per region, including terrestrial, freshwater and marine species. For islands, numbers are shown as dots for visualization. White areas on land denote that information is lacking. Note that the legend scale varies among panels (section **2.1.4** for further details about data sources and data processing). A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

2.3.2.2. Aquatic plants

Trends

The first records of alien aquatic plants date back to the eighteenth century, becoming more numerous by the early 1900s (Brundu, 2015b; Chomchalow, 2011; Gettys, 2019; M. P. Hill et al., 2020; Hussner et al., 2010). As modelled by Seebens, Bacher, et al. (2021), the rate of first records for alien aquatic plants increased post-1950, especially after 1980 when the ornamental plant trade increased (Hrivnák et al., 2019; Hussner et al., 2010; Nunes et al., 2015), and again after 2008 when aquatic detection improved with the development of environmental DNA technology. Both the numbers and rates of established alien aquatic plants are projected to continue to increase until 2050 (Seebens, Bacher, et al., 2021).

Status

Of the 13,168 established alien plant species reported in the GloNAF database, less than 1 per cent are aquatic (Pyšek, Pergl, et al., 2017). However, comprehensive assessments of aquatic alien plants globally are lacking. Still, some aquatic plant species are prominent invasive alien species. Originally from the tropical zone of South America, *Pontederia crassipes* (water hyacinth), is one of the world's most prevalent invasive alien aquatic plants. This free-floating vascular plant has invaded freshwater systems in 62 countries, from 40°N to 40°S (Pan et al., 2011) and, according to recent climate change models, its distribution may expand into higher latitudes as temperatures rise. It is prevalent in tropical and subtropical waterbodies where nutrient concentrations are often high due to agricultural runoff, deforestation, and insufficient wastewater treatment. There are no records of *Pontederia crassipes* first introductions, but many populations are well established and persistent despite control efforts (Coetzee et al., 2017; Villamagna & Murphy, 2010). Sheppard et al. (2006) provide an evaluation of several aquatic invasive alien plant species distributions and status in Europe. For example, *Azolla filiculoides* (water fern), a small annual floating fern (hydrophyte), became established in slow moving and still water in ponds, canals, dikes and lakes, following

escape from aquaria and botanical gardens in the mid-nineteenth century. The plant is now widespread in Central and Western Europe, South Africa, China and Australasia. Species from the Americas such as *Ludwigia grandiflora* (water primrose), *Ludwigia peploides* (water primrose), and aquatic perennial herbs (hydro-hemicryptophytes) are classified as invasive alien species in Europe. *Crassula helmsii* (Australian swamp stonecrop), originally from Australia and New Zealand, arrived in the United Kingdom in the 1950s and is known as an invasive alien species in the United Kingdom and the Kingdom of the Netherlands. *Elodea canadensis* (Canadian pondweed) and *Elodea nuttallii* (Nuttall's waterweed), both native to North America, are the most widespread alien aquatic plants in Europe. Introduced in the mid-1800s, *Elodea canadensis* spread along river systems throughout Europe in the latter half of the century and now occurs in many other countries worldwide. In the early twentieth century, *Elodea canadensis* was replaced by *Elodea nuttallii* in many regions. *Elodea nuttallii* may in turn begin to be replaced by another invasive alien hydrocharitacean species, *Lagarosiphon major* (African elodea), in the United Kingdom (Brundu, 2015a). *Myriophyllum aquaticum* (parrot's feather), from tropical and subtropical South America, is the dominant invasive alien aquatic plant in Europe. First introduced into France (1880) and then Portugal (1935) as an aquarium escapee, *Myriophyllum aquaticum* is also present in the United Kingdom and the Kingdom of the Netherlands and is probably more widespread as it was sold as an "oxygenating plant" until 2016. It is also a major weed in the United States, Australasia, Southern Africa, and Asia.

Among marine vascular plants, the seagrass *Zostera japonica* (dwarf eelgrass) was introduced to the Pacific Northwest in the mid-1900s likely via oyster aquaculture and has since spread and negatively impacted native *Zostera marina* (eelgrass) and ecosystem processes (Shafer et al., 2014). Additionally, *Halophila stipulacea* (halophila seagrass) was introduced to the Mediterranean Sea through the Suez Canal where it is now widespread (Willette et al., 2014). More recently, *Halophila stipulacea* was introduced to the Caribbean Sea where it is spreading and is described as the world's first globally invasive marine angiosperm (Willette et al., 2014; Winters et al., 2020).

2.3.2.3. Algae

In this section, algae are comprised of taxa of the phyla Rhodophyta, Chlorophyta, Charophyta, Cryptophyta, Euglenozoa, Haptophyta, Foraminifera, Ciliophora, Ochrophyta, Myzozoa and Cercozoa. Other groups of microorganisms are covered in **section 2.3.3**.

Trends

Globally, many alien green, brown, and red marine algae have been reported, with steep increases (**Figure 2.21**) in reports of large macroalgae invaders since the mid-twentieth century (Carlton & Eldredge, 2009; Fuentes et al., 2020; Ribera & Boudouresque, 1995; J. E. Smith, 2011; Vaz-Pinto et al., 2014; Villaseñor-Parada et al., 2018; S. L. Williams & Smith, 2007). The high rate of increase since this time likely reflects increased global shipping after the invention of containerized transport in 1956. A study on the global distribution of 97 marine algae with known invasion histories revealed that hotspots of future occurrences are in East Asian and European waters, largely reflecting high shipping intensities of enclosed seas (Seebens et al., 2016).

The unresolved tensions between using alien species for aquaculture and their potential ecological impacts are well-represented in the history of seaweed invasions. In the 1970s, a suite of alien seaweeds was introduced to the Hawaiian Islands for mariculture, including *Kappaphycus striatus* (Indo-Pacific red algae) and *Gracilaria salicornia* (red alga), and the tropical Atlantic *Hypnea musciformis* (hypnea). In subsequent decades, these algae spread across the Hawaiian Islands. *Kappaphycus* (red alga) is reported to achieve over 50 per cent cover on some Hawaiian coral reefs. Efforts to remove alien seaweeds from Hawaiian reefs are ongoing.

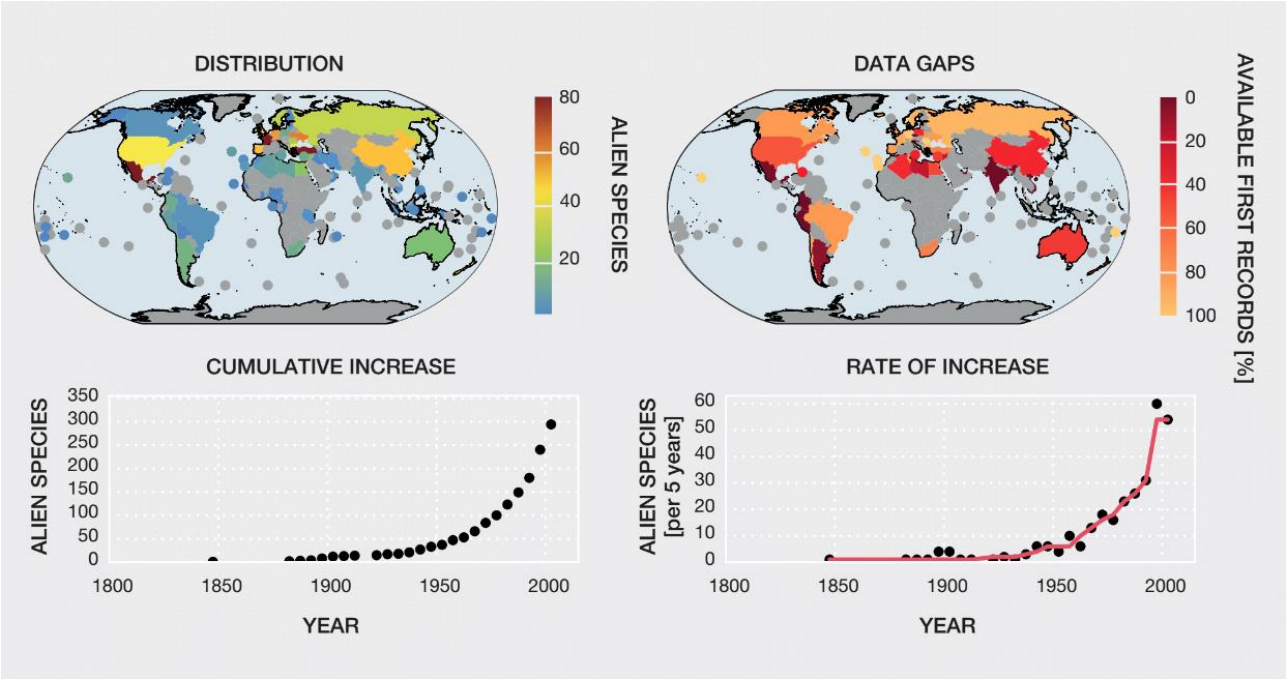

Figure 2.21. Status, trends, and data gaps for established alien algae. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (**section 2.1.4** for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (section **2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Examples of significant algal invasions with well-documented ecological and economic impacts include a variety of alien species native to Asia, such as *Sargassum muticum* (wire weed), *Codium fragile* (dead man's fingers), *Grateloupia turuturu* (devil's tongue weed), *Gracilaria vermiculophylla* (black wart weed), and *Asparagopsis armata* (Harpoon weed) – all now found on many continental margins around the world. Less widely distributed but even more notorious is *Caulerpa taxifolia* (killer algae), toxic to certain herbivores. More broadly distributed alien macroalgae are not necessarily more likely to succeed in new regions than more narrowly distributed species (S. L. Williams & Smith, 2007). For example, the genus *Capreolia* (red algae), considered endemic to Australasia, has been found on the coast of central Chile, based on molecular and morphological analysis (Boo et al., 2014). *Pyropia koreana* (red algae) described previously from Korea, has been reported in the Mediterranean Sea (Vergés et al., 2013) and New Zealand (Nelson et al., 2014) and was detected using molecular analysis. Finally, *Chondracanthus chamissoi* (yuyo), considered endemic to the south-central coast of Chile, has been reported, through molecular analysis, in France, Japan, and Korea, where it shows important morphological variations (M. Y. Yang et al., 2015; **Table 2.16**).

The cultivation of algae has facilitated the transfer of native species within country borders but still outside its historical range of distribution. For example, the macroalga *Gracilaria chilensis* (red seaweed), native to the south-central coast of Chile, has been extensively cultivated more than 640

km from its northern limit of distribution (Guillemin et al., 2008; Santelices, 1989), resulting in established alien populations from the escape of vegetative propagules from aquaculture facilities (Castilla & Neill, 2009; Guillemin et al., 2008; Villaseñor-Parada & Neill, 2011). Moreover, alien mollusc aquaculture has been identified as an introduction vector for many invasive macroalgae (Ribera Siguan, 2003; S. L. Williams & Smith, 2007). Indirect evidence suggests that several species of alien macroalgae have been introduced by aquaculture of *Magallana gigas* (Pacific oyster) in Europe (Krueger-Hadfield et al., 2017; Lang & Buschbaum, 2010; Mineur et al., 2007), North America (Mathieson et al., 2003) and South America (D. E. Bustamante & Ramírez, 2009; Croce & Parodi, 2014). Filamentous alien species such as *Polysiphonia morrowii*, or alien species with filamentous stages in their life cycle, such as the "*Falkenbergia* phase" of *Asparagopsis armata* (Harpoon weed) or the "*Vaucheroid* phase" of *Codium fragile* (dead man's fingers), benefit from the rugosities in the shell of *Magallana gigas* where they can pass unobserved.

Alien macroalgae species themselves can serve as an introduction vector for other alien species that live as epiphytes in the thallus. For example, in many ecosystems where *Codium fragile* (dead man's fingers) has been introduced, its most conspicuous epiphyte is the Asian macroalgae *Melanothamnus harveyi* (Harvey's siphon weed; e.g., González & Santelices, 2004; E. Jones & Thornber, 2010; Schmidt & Scheibling, 2006; Villaseñor-Parada & Neill, 2011). Apparently, *Melanothamnus harveyi* is a secondary introduction associated with *Codium fragile*. Native species may also play an important role in the spread of alien species. For example, *Schottera nicaeensis* (red algae) and *Asparagopsis armata* (Harpoon weed) are invasive alien species in the Pacific southeast coast, and they have been found as epiphytes in drifting thalluses of the buoyant macroalgae *Durvillaea antarctica* (cochayuyo), becoming a potential dispersal mechanism for these species (Macaya et al., 2016). For example, the release of reproductive fragments adrift has been identified as alternative dispersal strategies in *Codium fragile* (Villaseñor-Parada et al., 2013) and *Mastocarpus latissimus* (Oróstica et al., 2012).

Table 2.16. Top 10 most widespread invasive alien algae species worldwide

The number of regions where the species is recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien algae species rather than their impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	No. of regions	Species	No. of regions
***Undaria pinnatifida* (Asian kelp)**	9	*Gracilaria vermiculophylla* (black wart weed)	5
***Sargassum muticum* (wire weed)**	8	*Coscinodiscus wailesii* (diatom)	5
***Caulerpa taxifolia* (killer algae)**	7	*Dasysiphonia japonica* (siphoned Japan weed)	5
***Caulerpa cylindracea* (green algae)**	6	*Alexandrium tamarense* (dinoflagellate)	4
***Codium fragile* (dead man's fingers)**	6	*Alexandrium minutum* (dinoflagellate)	4

2.3.2.4. Bryophytes

Trends

Cumulative numbers of first records grew slowly until 1950 and have since increased rapidly worldwide (**Figure 2.22**), particularly in Oceania and Europe (Essl et al., 2013).

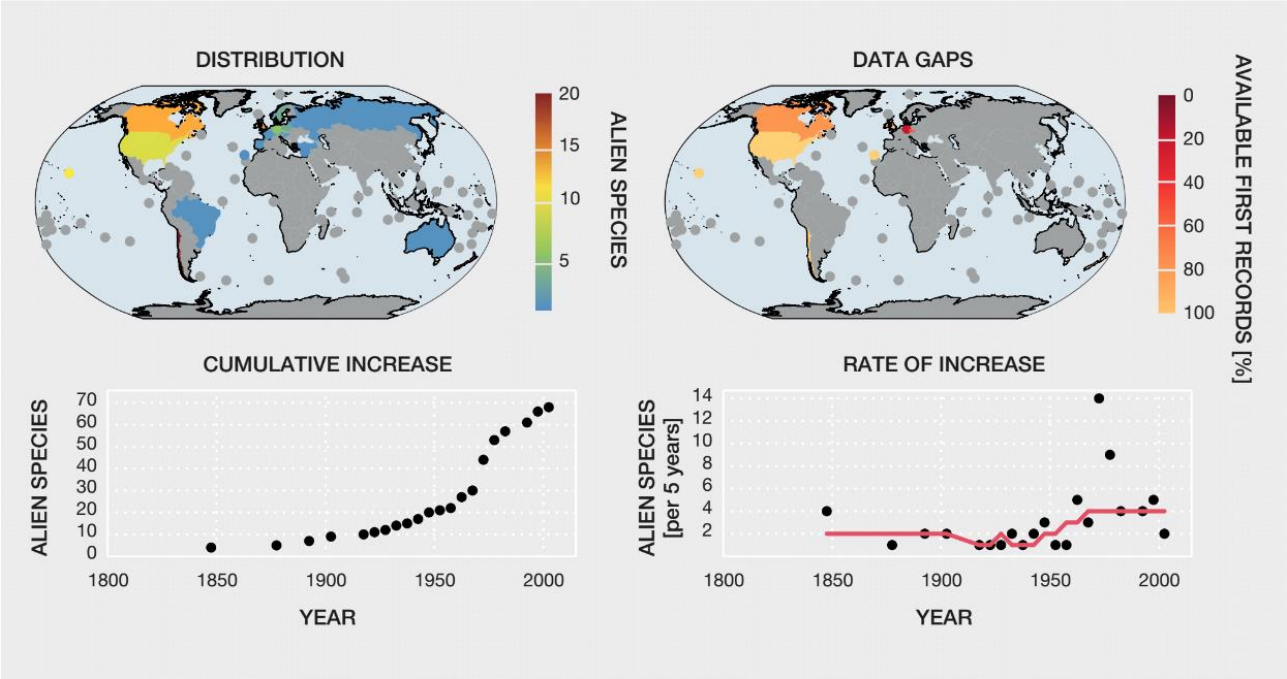

Figure 2.22. Status, trends, and data gaps for established alien bryophytes. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (**section 2.1.4** for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend line is calculated as running median (**section 2.1.4** for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

The most comprehensive assessment of alien bryophytes compiled data from 82 locations on five continents in both hemispheres (Essl et al., 2013). To date, 139 species of bryophytes are considered alien in at least one of the regions studied, of which 79 are established, 19 are casual and 41 are cryptogenic (of uncertain origin; G**lossary**) occurrences. Of these, 106 are mosses, 28 liverworts, and 5 hornworts. Only 18 species (i.e., 13 per cent) are recorded as alien from at least five regions, with the most widespread being *Campylopus introflexus* (heath star moss; the best documented invasion, introduced to the United Kingdom in 1941 and coastal Europe in 1954 and currently extending to Russia in the east and the Mediterranean in the south), *Kindbergia praelonga* (common feather moss), *Lunularia cruciata* (crescent-cup liverwort), *Orthodontium lineare* (cape thread-moss), and *Pseudoscleropodium purum* (neat-feather moss). The two most important pathways for bryophyte introductions are unintentional imports as hitchhikers on ships and planes and as epiphytes on ornamental plants and other horticultural supplies with 34 and 27 species, respectively. Most alien bryophytes occur in human-made habitats, such as ruderal sites, roadsides,

and lawns, while only a few natural ecosystems such as forests and rocky outcrops regularly harbour alien bryophytes (Essl et al., 2013).

Among locations of the Northern Hemisphere, the highest numbers of alien bryophytes are recorded for the Hawaiian Islands, United States and United Kingdom (22 species), followed by British Columbia, Canada (13 species), Ireland (11 species), California, United States (10 species) and France (10 species). In the Southern Hemisphere, most alien bryophyte species are recorded on islands (South and North Islands of New Zealand, 27 species each; St. Helena, 22 species). Continental South America, Asia and Africa have much lower numbers of alien bryophytes, from three to six species (Essl et al., 2013). In general, islands are more invaded by alien (and cryptogenic) bryophytes than continental regions (Essl et al., 2013). For invasive alien bryophytes, GRIIS (Pagad et al., 2022) lists only two species that occur in more than one region, *Campylopus introflexus* (heath star moss) and *Orthodontium lineare* (cape thread-moss), each occurring in two regions.

2.3.2.5. Data and knowledge gaps

The GloNAF database and associated analyses (Pyšek, Pergl, et al., 2017; van Kleunen et al., 2015, 2019) make it possible to quantify the proportion of a continental area for which data on established alien vascular plants are available (e.g., **Box 2.2**). GloNAF 1.1 covers more than 83 per cent of the world's ice-free terrestrial surface in terms of regions (n = 843) for which alien floras are available, but there is great variation in the geographic coverage among the continents defined by the Biodiversity Information Standards (TDWG, 2021). There is nearly complete data coverage, in terms of the proportion of individual regions having data on their alien floras, for Australasia (99.5 per cent of regions at the country, state, district or island level have information on alien flora), Africa (98.6 per cent), North America (95.9 per cent), South America (95.8 per cent) and Antarctica (90.2 per cent). The continents with lower coverage are tropical Asia (68.5 per cent), and particularly temperate Asia (54.8 per cent), where data are missing primarily for parts of Russia. The lack of data on alien floras for some regions of the European part of Russia also results in rather low coverage for Europe as a whole (63.8 per cent of the continent area). Data on alien plants are available for about half of the total area of the Pacific islands (49.1 per cent). However, good geographical coverage does not mean the information on the alien plants for a given region is complete; there can be data gaps even for well-studied regions (Pyšek et al., 2008), as well uncertainties about a species status. Notably, identification of alien species is challenging for taxa with a distribution over more than one continent, for which no global identification key is available, and especially when the origin of the alien plant is unknown, such as for Cyperaceae, *Hydrocotyle* or *Myriophyllum*. The quality and completeness of individual datasets also vary greatly, as does the assessment of the status of alien species, habitat affiliations, first records and pathways (**Figure 2.22**). Ideally, records of alien plants occurrences would be collected following broadly accepted standards that reflect the research infrastructure and resources (Latombe et al., 2017; **Chapter 6**, **section 6.6.2.3**).

Similarly, comprehensive databases such as the GloNAF database are not available for bryophytes or algae, severely limiting the potential for a thorough assessment of the trends and status for these groups. While alien bryophytes in Central and Western Europe and North America are well-documented, data on alien bryophytes on all other continents, and particularly in the tropics, are rarely available (Essl et al., 2013). The number of algal invasions worldwide is poorly known due to low research efforts. In addition, comparatively high taxonomic uncertainty makes it difficult to compare species identities among studies. Many hundreds of seaweed species bear the same name around the world but are regarded as naturally distributed. These species doubtless represent a mixture of species complexes peppered with many overlooked invasions. Furthermore, the original native ranges are often unknown, making it impossible to determine whether populations are native or alien in that region. As a consequence, many populations of algae and bryophytes species can

only be classified as cryptogenic and a comprehensive assessment of the current status of their alien distributions remains elusive.

Finally, the aforementioned databases provide regional lists of alien taxa without information on their precise spatial distributions. In large countries it is especially common that a reported species occurs in only part of the country. Occurrence datasets like the GBIF hold such spatially explicit data but to date report only incomplete information on the biogeographic status of taxa, that is, whether a species is native or alien (C. Meyer et al., 2016). Additionally, like all global databases, GBIF records for plants are biased in terms of taxonomy, space, and time (A. C. Hughes et al., 2021; C. Meyer et al., 2016; Troudet et al., 2017). However, new methods are emerging that allow the use of probabilistic tools to estimate the biogeographic status of occurrence records (Arlé et al., 2021).

2.3.3. Fungi and microorganisms

This section reports on the temporal trends and status of the distribution of alien and invasive alien species for fungi (**section 2.3.3.1**) and the group of Chromista, bacteria and viruses (**section 2.3.3.2**) as well as data and knowledge gaps (**section 2.3.3.3**). In this chapter the group of microorganisms is split into "fungi" (**section 2.3.3.1**) with the phyla Ascomycota, Chytridiomycota, Basidiomycota, Microsporidia, and Zygomycota, and "Chromista, bacteria and viruses" (**section 2.3.3.2**) with the taxonomic groups Oomycota, Actinobacteria, Chlamydiae, Cyanobacteria, Firmicutes, Proteobacteria, and viruses. Other groups of microorganisms are covered in **section 2.3.2.3**. Note that there can be a high degree of uncertainty about to the status of microorganisms as native or alien.

2.3.3.1. Fungi

Trends

Fungi comprise an immensely diverse biological kingdom that forms complex interactions at multiple ecological levels. Fungal invasions are increasingly recognized as key drivers of wildlife mortality and population declines for amphibians, bats, bees, soft coral, and other organisms (Fisher et al., 2012). Introduction of undesirable alien fungi such as those producing repellent smells or toxic compounds, is also problematic (Parent et al., 2000; A. Pringle & Vellinga, 2006). Negative impacts of plant diseases caused by fungal invasions have resulted in widespread ecosystem disruptions that indirectly impact the function of forests, streams, and other natural environments (Anderson et al., 2004; Scott et al., 2019; **Chapter 4**, **section 4.3.1**) such as *Hymenoscyphus fraxineus* (ash dieback; **Table 2.17**) causing ash dieback in Europe. In addition, alien fungal pathogens have severe negative impacts on agricultural crops (**Chapter 4**, **section 4.4.1**). Examples include *Phytophthora ramorum* (sudden oak death; Thakur et al., 2019), *Phyllosticta citricarpa* (citrus black spot; Guarnaccia et al., 2019), *Phakopsora pachyrhizi* (soybean rust; Dean et al., 2012) or *Pyricularia oryzae* (rice blast disease; Fones et al., 2020).

With an increasingly connected world, the rate at which alien fungi are recorded is accelerating (Bebber et al., 2013; Desprez-Loustau, 2009; Fisher et al., 2012). First reports (**Figure 2.23**) of alien fungi have increased consistently since the mid-1800s (Bebber et al., 2013; Fisher et al., 2012; Monteiro et al., 2020; Santini et al., 2013), with approximately 25 per cent of all dated records reported since 2000 (Monteiro et al., 2020). New species discovery for fungi has risen from 1,000-1,500 per year in the mid-2000s, to a peak of more than 2,500 species in 2016 and over 2,000 new species discovered in 2019 (Cheek et al., 2020). Nonetheless, reports of new occurrences are almost certainly underestimated (Bebber et al., 2019). In addition, with rising temperatures and more frequent extreme weather events, fungi are not only able to invade novel geographical areas, but some potentially pathogenic species are also beginning to evolve levels of thermotolerance that

could allow them to breach the thermal barriers that have long protected mammals from fungal infections, representing a further threat to human health and wellbeing (Nnadi & Carter, 2021).

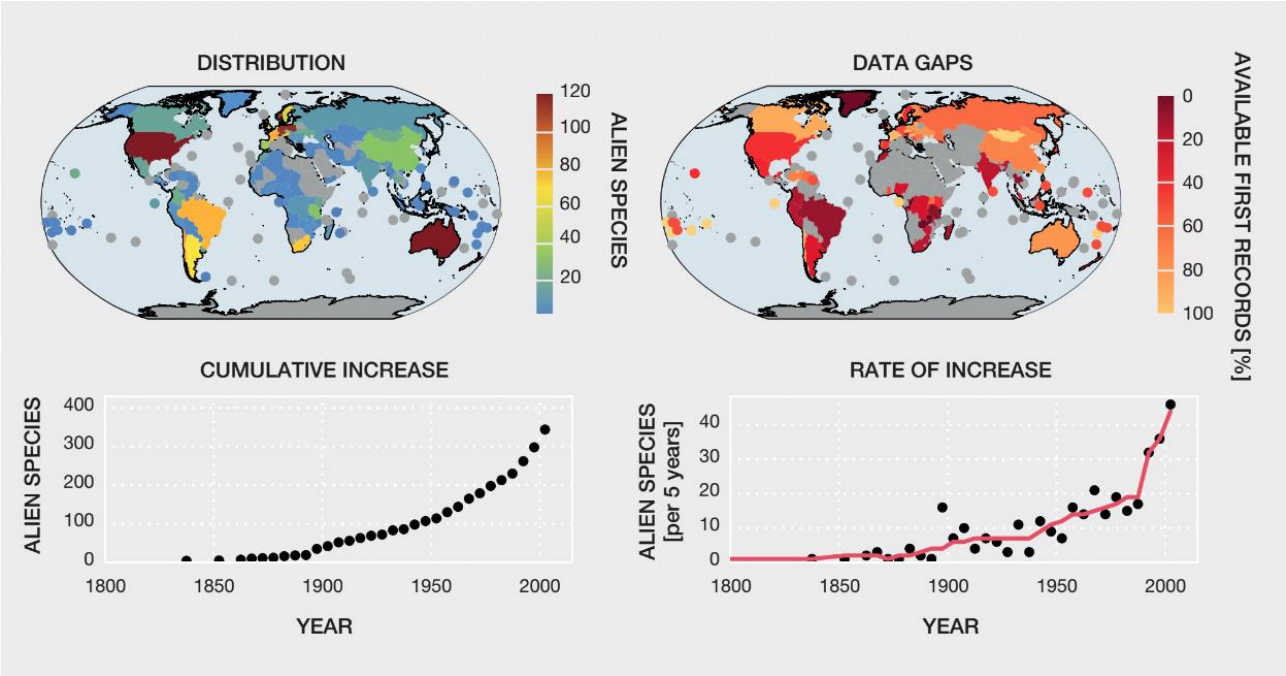

Figure 2.23. Status, trends, and data gaps for established alien fungi.
The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (**section 2.1.4** for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (**section 2.1.4** for further details about data sources and data processing). Note that presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Fungi are widely dispersed by humans, often unintentionally or as stowaways, via transport through the trade of goods such as plants, seed, wood, shipping containers and other materials (Desprez-Loustau, 2009). Fungi are also dispersed across long and short distances in the atmosphere by wind or water and weather disruptions can play a significant role in spreading fungi into new regions (Anderson et al., 2004; J. K. M. Brown & Hovmøller, 2002). Fungi are being recorded on all continents, including Antarctica (**Figure 2.23**).

The fungi comprise an immensely diverse biological kingdom that forms complex interactions at multiple ecological levels. Their inconspicuous nature and dispersal by small, often long-lived spores make the spread of fungi to new locations difficult to control and easy to overlook. Fungal size, particularly the size of the fungal spore-bearing structures, greatly influences how invasive alien fungi are recognized and studied (Desprez-Loustau et al., 2010). The "microfungi," so called because their spore-bearing structures are microscopic, are the most important fungi associated with plant diseases. In contrast, the "macrofungi", which produce large and sometimes vividly coloured spore-bearing structures (e.g., mushrooms), are mostly saprophytes and ectomycorrhizal fungi. Although the distinction between macro and microfungi is artificial, fungal size alone does influence the assessment of invasion dynamics of invasive alien fungi.

About 650 species of macrofungi have been recorded outside their native ranges (Monteiro et al., 2020). Most belong to the orders Agaricales (44 per cent) and Boletales (29 per cent); slightly more than half are ectomycorrhizal, and the remainder are saprotrophic (Monteiro et al., 2020). The most widely distributed alien macrofungi include *Amanita muscaria* (fly agaric), *Amanita phalloides* (death cap), *Phellinus noxius* (brown tea root disease), *Suillus granulatus* (weeping bolete mushroom), and *Suillus luteus* (ectomycorrhizal fungus of pine) (Monteiro et al., 2020). The highest known diversity of macrofungal alien species is in the Southern Hemisphere in countries such as Argentina, Brazil, Chile, New Zealand, and South Africa, and in several European countries, including France, Germany, and the United Kingdom (Monteiro et al., 2020; Vellinga et al., 2009).

Invasive alien fungal symbionts have been co-introduced with their hosts, as in the case of the ectomycorrhizal fungus *Amanita phalloides* (death cap), a native of Europe introduced to Australia and North and South America, probably in soils as consequence of the plant trade (A. Pringle et al., 2009; Vellinga et al., 2009; A. Pringle & Vellinga, 2006). According to Vellinga et al. (2009), about 200 species of ectomycorrhizal fungi (including ascomycetes and basidiomycetes) have been introduced into novel habitats due to the transport of *Eucalyptus* and *Pinus* spp. (Pine).

Dung fungi that have accompanied their herbivore partners introduced to the Caribbean islands are a good example (M. J. Richardson, 2008). Commercial use of "biofertilizers" based on arbuscular mycorrhizal fungi is another example. This has led to a global spread of these species (Thomsen & Hart, 2018). Although they can have long-term effects on ecosystems, such alien species tend to go unnoticed (Velásquez et al., 2018) or, in the case of "biofertilizers", unrecognized as an invasion. Some unnoticed alien fungal species may be mutualists associated with only one symbiont species, for example as a plant endobiont. If that symbiont is itself an invasive alien species, a case can be made that the unnoticed mutualist too is behaving invasively by contributing to the success of its associated invasive alien plant. Therefore, an as yet unknown number of additional fungal invasive alien species may remain undetected.

Most parasitic fungi affect plants (Anderson et al., 2004). Examples of invasive alien species include *Cryphonectria parasitica* (blight of chestnut; Gruenwald, 2012), *Ophiostoma* spp. including *Ophiostoma novo-ulmi* (Dutch elm disease; Brasier & Kirk, 2000), *Cronartium ribicola* (white pine blister rust), *Austropuccinia psidii* (myrtle rust), and *Discula destructiva* (dogwood anthracnose). More aggressive genotypes of known plant pathogenic fungi may also arrive as alien species and later become invasive (Arenz et al., 2011). Also important are invasive alien oomycetes such as *Phytophthora pinifolia* causing needle disease in *Pinus radiata* (radiata pine) in Chile (Durán et al., 2008) and hybridization of oomycetes in the genus *Phytophthora* that can cause serious damage to agriculture, horticulture, and Forestry (Érsek & Nagy, 2008).

Alien and invasive alien fungi that are pathogenic to animals include *Batrachochytrium dendrobatidis* (chytrid fungi) and *Batrachochytrium salamandrivorans* (chytrid fungi) which are the agents of chytridiomycosis, a disease spread by trade and causing massive global amphibian declines (Berger et al., 2016; Weldon et al., 2004), and *Pseudogymnoascus destructans* (white-nose syndrome fungus) in bats (Hendrix & Bohlen, 2002; Hovmøller et al., 2016; Sikes et al., 2018; Thakur et al., 2019)

Table 2.17. Top 10 most widespread invasive alien fungi worldwide

The number of regions where the species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien species rather than their impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed

occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	No. of regions	Species	No. of regions
***Ophiostoma novo-ulmi* (Dutch elm disease)**	10	*Ophiostoma ulmi* (Dutch elm disease)	4
***Batrachochytrium dendrobatidis* (chytrid fungus)**	9	*Erysiphe alphitoides* (oak mildew)	3
***Cryphonectria parasitica* (blight of chestnut)**	5	*Melampsoridium hiratsukanum* (alder rust)	3
***Hymenoscyphus fraxineus* (ash dieback)**	5	*Clathrus archeri* (devil's fingers)	2
Pyrrhoderma noxium	5	*Cronartium ribicola* (white pine blister rust)	2

2.3.3.2. Chromista, bacteria, protozoans, and viruses

Chromista and other eukaryotic protists constitute several biological kingdoms independent of those for animals, fungi, and plants. Their underlying phylogeny remains poorly understood, with classifications frequently and often radically changing as molecular evidence becomes available. Chromista includes major groups of ecologically highly significant organisms, including many marine algae, diatoms and oomycetes. Note that some groups of Chromista, which are usually considered algae, are addressed in section "Algae" (**section 2.2.2.3**). Here, taxa of the groups Oomycota, Actinobacteria, Chlamydiae, Cyanobacteria, Firmicutes, Proteobacteria and viruses are included.

Along with the true fungi, the Oomycota (with few exceptions including Phytophthora) have rarely been analysed within the context of biological invasions. Recent advances in molecular analyses, however, have shown that at least some of these species have defined natural distributions and can be considered alien if introduced by humans beyond the native range. The emergence of microbial invasive alien species, pathogenic or not, is thus a global phenomenon and a major threat in invasion ecology (Jack et al., 2021; Litchman, 2010; Mawarda et al., 2020; Ricciardi et al., 2017; Thakur et al., 2019).

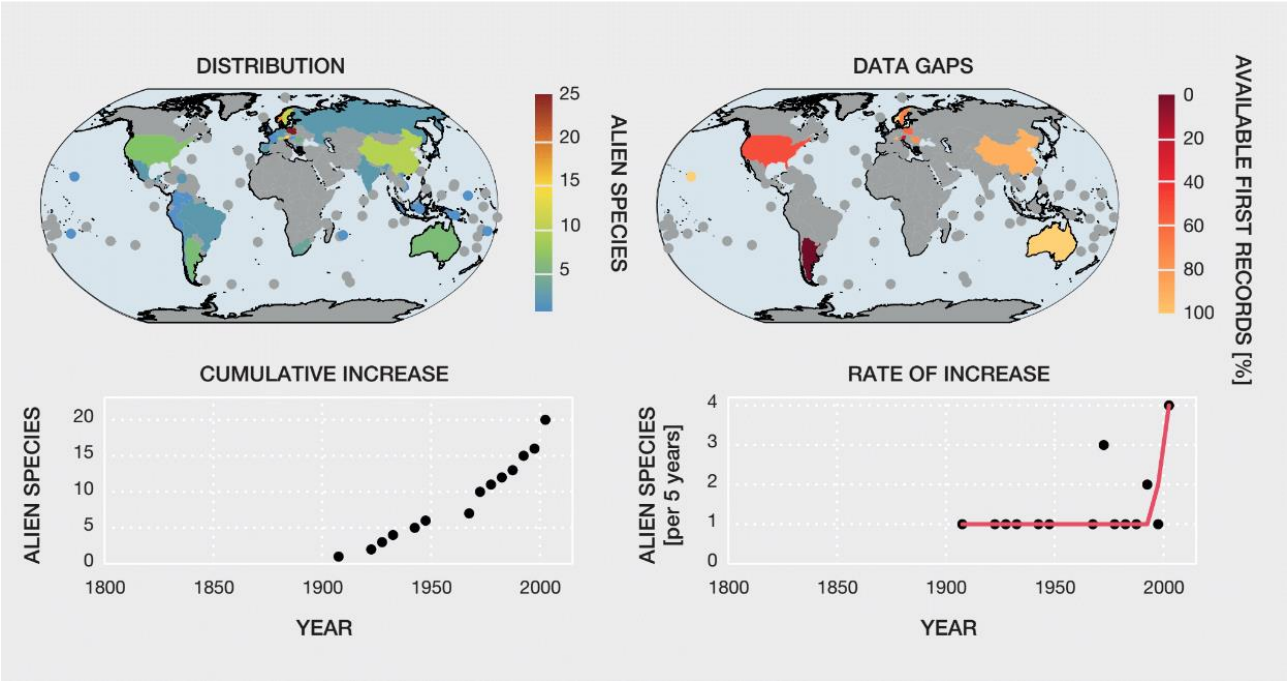

Figure 2.24. Status, trends, and data gaps for established alien oomycetes. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region (**section 2.1.4** for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (**section 2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Trends

The numbers of alien oomycetes have risen continuously since 1900 (**Figure 2.24**; Santini et al., 2013), as has the numbers for other alien microorganisms as well (**Figure 2.25**). The new arrivals include some species which are causal agents of serious plant diseases (Blehert et al., 2009; Fisher et al., 2009; Robert et al., 2012; Singh et al., 2008). Global trade is a major driver of oomycete invasions as they are usually unintentionally introduced on their hosts or as contaminants of goods (Sikes et al., 2018). In particular, plants transported with intact root systems, and particularly with soil, are likely to host potentially alien oomycete species, both beneficial and pathogenic.

Historically, there have been several oomycete invasions that have had huge impacts on humans. The most prominent is *Phytophthora infestans* (Phytophthora blight) introduced in the 1800s from North America to Europe. The dispersal of *Phytophthora infestans* is well documented with multiple periods of intense spread over the past 200 years (Fry, 2008). It was the main cause of repeated total potato crop failures resulting in massive famines with millions of deaths and a huge wave of emigration by hundreds of thousands of Europeans (Woodham-Smith, 1962; Yoshida et al., 2013). Importantly, *Phytophthora* species can hybridize, attain greater vigour, and potentially infect a wider host range relative to parent species thereby creating a serious threat to managed and natural systems (Van Poucke et al., 2021).

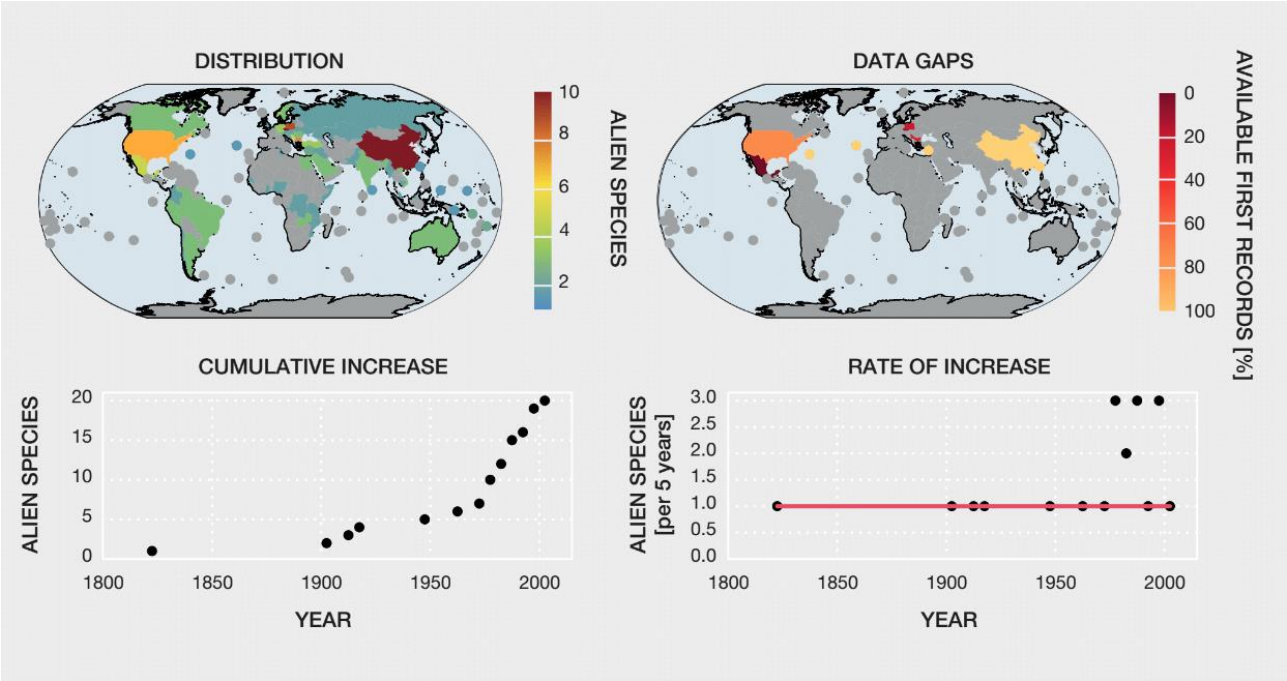

Figure 2.25. Status, trends, and data gaps for established alien Chromista, bacteria, protozoans, and viruses. The number of established alien species per region (upper left) and the amount of available data (upper right) are indicated by colour. The amount of available data is estimated by the proportion of available first records among all records available for that region **(section 2.1.4** for further details). Grey regions denote areas with lacking data. Oceans are tinted for visualization and do not indicate species numbers. Trends are shown in lower panels for cumulative numbers and as a rate of increase (i.e., numbers of established alien species per five years). Smoothed trend (line) is calculated as running median (**section 2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Well-documented microbial invaders are typically pathogenic organisms which are detected because of their devastating impacts. Anderson et al. (2004) provided a list of emerging infectious diseases including *Phytophthora ramorum* (sudden oak death; Gruenwald, 2012).

Biological invasions caused by viruses are also extremely relevant in the context of plants as they account for almost 50 per cent of their emerging infectious diseases (Anderson et al., 2004). In many cases they are transmitted by an invasive alien host species such as *Bemisia tabaci* (tocacco whitefly), which can transmit over 114 virus species (D. R. Jones, 2003). Despite its tropical origin, there have been outbreaks of *Ralstonia solanacearum* biovar 2 (brown potato rot) in Europe where it survives the winter in waterways in association with endemic plants (Stevens & van Elsas, 2010). Many pathogenic microbes are thought to be alien species in the areas in which they were found (Rúa et al., 2011).

Detection of non-pathogenic microbial species is more difficult because their impacts can be more subtle and do not result in mortality or disease and are therefore harder to quantify unless previously identified impacts are specifically looked for. Co-invasion of non-pathogenic microbes with plants has been detected in California, United States where genomic analyses revealed that *Ensifer medicae*, a bacterial symbiont associated with the legume *Medicago polymorpha* (bur clover), was introduced from Europe (Porter et al., 2018). Similarly, colonization of New Zealand

by European *Lotus corniculatus* (bird's-foot trefoil) coincides with the introduction of its symbiotic partner, the bacterium *Mesorhizobium loti* (Sullivan et al., 1995, 1996).

In most cases, it is unknown whether these introductions spread to other hosts in the introduced habitats which might potentially lead to the displacement of native symbiotic species. Although most known microbial introductions have been reported from Europe, South America, Australia, and New Zealand, these data might be biased by the number of papers published from each country (Vellinga et al., 2009). **Table 2.18** lists the 10 most widespread invasive alien Chromista and bacteria and the number of regions each has invaded.

Table 2.18. Top 10 most widespread invasive alien taxa of the groups Chromista and bacteria worldwide

The number of regions where the respective species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note that this table only refers to the distribution of invasive alien species rather than their impacts which are covered in **Chapter 4** (see **section 2.1.4** for further details on data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species	No. of regions	Species	No. of regions
***Vibrio cholerae* (cholera)**	17	*Phytophthora cambivora* (root rot of forest trees)	3
***Aphanomyces astaci* (crayfish plague)**	13	*Phytophthora cactorum* (apple collar rot)	2
***Phytophthora cinnamomi* (Phytophthora dieback)**	5	*Phytophthora gonapodyides* (oomycetes)	2
***Phytophthora ramorum* (sudden oak death)**	4	*Phytophthora infestans* (Phytophthora blight)	2
***Yersinia pestis* (black death)**	4	*Phytophthora plurivora* (oomycetes)	2

2.3.3.3. Data and knowledge gaps

Data and knowledge gaps for fungi are vast. Fungi are frequently unnoticed or unreported, particularly in regions where scientific infrastructure is minimal (Desprez-Loustau et al., 2010). Information about alien fungi in different regions can vary tremendously, with biases associated with available scientific infrastructure, taxonomic expertise, crop production, and trade routes (Desprez-Loustau et al., 2010; Lofgren & Stajich, 2021). There are generally far fewer records of fungi than for animals and plants, even from areas with a strong tradition of fieldwork. There are several estimates of the total number of fungal species, with values ranging from 2.2 to 5.1 million, to as many as 11.7 to 13.2 million species (Lofgren & Stajich, 2021). These millions of predicted fungal species greatly eclipse the 146,155 species that are so far discovered and named (Kirk, 2021) and indicate that as many as 98.8 per cent of all fungal species await discovery. Although the rate of new species discoveries has accelerated since the advent of DNA technologies, at the current rate of about 2,000 new fungal species described each year (Cheek et al., 2020), it will be at least a thousand years before a comprehensive inventory of fungal diversity is made.

The continued paucity of rapidly accessible and reliable information for fungi remains a major hurdle for identifying new fungal invasive alien species, particularly cryptogenic fungi, as their initial establishment phase, which is the only stage at which effective countermeasures are feasible, often remains unnoticed until major damage is done (McMullan et al., 2018). Another important knowledge gap is an insufficient understanding of the taxonomic limits of fungal species. This hinders effective quarantine of animal and plant pathogens. Using molecular phylogenetics, several

disease-causing microfungi were found to belong to species complexes, and incorrect identifications have led to confusion (Coleman, 2016; X. Lin & Heitman, 2006; Thines & Choi, 2016).

As with fungi, only 10 per cent of all probable oomycete species are estimated to be known and described (Thines, 2014), a large knowledge gap. Information about non-terrestrial species is similarly limited, although several invasions by aquatic algae have been documented (Acosta et al., 2015), including the *Prymnesium parvum* (golden algae) which has successfully established in freshwater ecosystems in several locations in the United States (Roelke et al., 2016; see also **section 2.2.2** including Algae).

Box 2.3. Evolution during biological invasions

Biological invasions have been instrumental in demonstrating that evolution can be rapid enough to contribute to contemporary ecological dynamics and that feedback between ecology and evolution can occur within a few generations (so-called "eco-evolutionary dynamics"; Carroll et al., 2007; Hendry, 2020). Evolution can influence the trends and status of biological invasions by enhancing dispersal rates that lead to species range expansion, improving alien species' performance, and increasing adaptation to novel environments (Suarez & Tsutsui, 2008; Vellend et al., 2007). Indeed, approximately half of the investigated plants and animals show increased size and fecundity in their new range (Parker et al., 2013); many of these differences are likely to have a genetic basis. Adaptive evolution (i.e., evolutionary changes that increase the chance of survival and reproduction) is thought to be common for alien species, especially alien plants (Hodgins et al., 2009). A well-known animal example is *Rhinella marina* (cane toad), which has evolved longer legs and faster movement as its alien range has expanded across Australia (Phillips et al., 2006).

Observations of evolution during invasion initially presented researchers with a paradox. Newly introduced populations tend to be small and are therefore expected to contain low genetic diversity, thereby limiting the population's ability to respond to selection (Sakai et al., 2001). However, some populations that undergo founder effects and genetic bottlenecks can evolve rapidly (Dlugosch & Parker, 2008). In fact, low genetic variation can facilitate invasive behaviour. For example, loss of genetic variation may have reduced intraspecific aggression among alien populations of *Linepithema humile* (Argentine ant), leading to the formation of competitively dominant "supercolonies" (Tsutsui et al., 2000). Other successful invasive alien species have been introduced multiple times and in high numbers (i.e., high propagule pressure), offsetting founder effects and limiting genetic bottlenecks (Roman & Darling, 2007). Indeed, introductions of individuals from different parts of a species' native range can create genetic admixtures (a mixture of previously distinct genetic lineages), boosting levels of standing genetic variation in the new range (Meyerson & Cronin, 2013) and potentially providing fitness advantages through hybrid vigour and increased variation, on which selection can act (S. R. Keller & Taylor, 2010). The contribution of novel mutations in large invasive alien populations also cannot be discounted (Colautti & Lau, 2015).

Hybridization and introgression

Genetic variation can also be enhanced during invasion by hybridization among species and interbreeding between native and introduced genotypes (Meyerson et al., 2010; Meyerson & Cronin, 2013); these mechanisms occur commonly and can play an important role during invasion (Hovick & Whitney, 2014; Largiadèr, 2008). Hybridization can facilitate successful invasions if it is beneficial and increases fitness (Bossdorf et al., 2005; Ellstrand & Schierenbeck, 2000; Meyerson et al., 2010; Rius & Darling, 2014); and may help a species overcome Allee effects associated with small sizes of introduced populations (Yamaguchi et al., 2019). For example, hybridization between *Sporobolus alterniflorus* (smooth cordgrass), which was deliberately introduced to the North American Pacific coast from its Atlantic-coast native range, and native *Sporobolus foliosus*

(California cordgrass) have generated highly invasive hybrid populations (Daehler & Strong, 1997). Particularly in plants, polyploidy (i.e., genome duplication), sometimes in association with hybridization (Strong & Ayres, 2013), is linked with the success of some alien species through several mechanisms, including enhanced genetic variability (Suda et al., 2015; te Beest et al., 2011). Nonetheless, how frequently the benefits of hybridization outweigh the negative effects is still poorly understood (Hodgins et al., 2018).

Plasticity and adaptation

Invasive alien populations with low genetic variation can also respond to environmental variation in a new range through phenotypic plasticity (Torchyk & Jeschke, 2018). Through plasticity, a single genotype can undergo physiological, phenological, and morphologic changes in response to environmental conditions, which can have significant evolutionary implications (Schlichting, 1986). While it is expected that plasticity will support the establishment and spread of alien species introduced to novel environments (Richards et al., 2006), support for the hypothesis that invasive alien species display greater plasticity than native or non-invasive alien species is mixed (A. M. Davidson et al., 2011; Meyerson et al., 2020; Palacio-López & Gianoli, 2011; Torchyk & Jeschke, 2018). Phenotypic variation can also be generated during invasions through epigenetic mechanisms, that is heritable DNA modifications without changes in the genetic code (Bossdorf et al., 2008). While epigenetic variation has been associated with some successful invasions (C. Liu et al., 2020; Richards et al., 2012), it is too early to generalize about the importance of this mechanism for invasions (Bock et al., 2015). Invasive alien species can also adapt to environmental conditions in their new range and increase their abundance, though few empirical studies have quantified these links (Hodgins et al., 2018). For example, *Lythrum salicaria* (purple loosestrife) in North America has experienced demographic benefits of adaptation estimated to be equivalent to those that the species enjoys from natural enemy release (Colautti & Barrett, 2013).

Data and knowledge gaps

A key uncertainty is how much evolution favours or hinders the outcome of a biological invasion, for example, by making the difference between invasion success and failure (Bock et al., 2015). To this end, perspectives from ecology and evolution could be further integrated by combining genomic tools with more classical experimental and comparative studies to test the mechanisms and consequences of evolution during invasion (Holman et al., 2019; McCartney et al., 2019). Another critical question is to what extent evolution allows alien species to colonize environments that are outside of their native-range ecological niches (Moran & Alexander, 2014; Pearman et al., 2008). Settling this question is important for commonly used tools such as species distribution models to forecast potential distributions of alien species (Pearman et al., 2008). Finally, studies of invasions have shown that some species can rapidly adapt to changing environments (Colautti & Lau, 2015; Hodgins et al., 2018). Alien species may be exceptionally responsive to interacting global-change drivers (Moran & Alexander, 2014), such as climate change or land-use change, a topic warranting further research (**Chapter 3, sections 3.5** and **3.6.1**).

Linking evolution and molecular tools to invasive alien species impacts and management

Just as alien species adapt to their novel environments, so too have native species evolved in response to the novel selection pressures posed by alien species. Evolutionary responses to exposure to alien competitors appear to be widespread in plants (Oduor, 2013). Thus, evolution may partially mitigate the negative impacts of invasive alien species on native communities (Carroll, 2011). This understanding also points to ways in which genetic tools and evolutionary principles may help to mitigate some of the impacts of invasive alien species (Chown et al., 2015; Lankau et al., 2011).

Information about the evolutionary/phylogeographic history of alien species obtained by using molecular markers and up-to-date statistical methods can also have several practical benefits for alien species monitoring and management (Lankau et al., 2011). Such knowledge can improve the efficacy of biocontrol programmes by targeting biocontrol agents from within the source region of a given invasive alien species (Chown et al., 2015) and provide better delimitation of source regions and introduction pathways, which can be obtained using high-resolution genomic tools (Hudson et al., 2021, 2022). While it is widely recognized that biological invasions constitute a natural experimental framework for the study of contemporary evolution, a good understanding of source regions and introduction pathways (i.e., routes of invasion/introduction) is essential. Knowledge of those routes makes it possible to precisely compare introduced populations to their original source population(s) and thus determine whether the invaders have, for example, undergone an adaptive change that has favoured them in their new living environment. This change may result from the selection of genetic variants that are rare in the original source population(s) but favoured in the new environment. The reconstruction of routes of invasion/introduction is, therefore, crucial to define and test different hypotheses concerning the environmental and evolutionary factors underlying biological invasions and their success (Estoup & Guillemaud, 2010; S. R. Keller & Taylor, 2008). Bulk screening by using metabarcoding approaches may be used to flag recognized invaders at ports of entry and so prevent the introduction of harmful species (or new genotypes of already introduced species). The potential for molecular instruments to detect the spread of invasive alien species is important, although many challenges remain (Handley, 2015).

2.4. Trends and status of alien and invasive alien species by IPBES regions

This section reports on the temporal trends and status of the distribution of alien and invasive alien species across IPBES regions (**section 2.4.1**), and for the individual IPBES regions Africa (**section 2.4.2**), the Americas (**section 2.4.3**), Asia and the Pacific (**section 2.4.4**), and Europe and Central Asia (**section 2.4.5**), and their respective sub-regions. A description of IPBES regions and sub-regions including a spatial representation is provided online (IPBES Technical Support Unit On Knowledge And Data, 2021) and in **Chapter 1**, **section 1.6.4**. For each IPBES region, dynamics on islands and data and knowledge gaps are provided as well. A global synthesis on the dynamics on islands and in protected areas is provided in boxes (**Boxes 2.4** and **2.5**).

2.4.1. Overview of trends and status by IPBES regions

Trends

The number of established alien species records has increased for all taxonomic groups and for all IPBES regions since 1500 with particularly steep escalations observed after 1800 (**Figure 2.26**). Before 1800, the number of records is particularly low for insects and crustaceans. However, this is likely because of the lack of data, which is particularly common for invertebrate groups (**section 2.3.1.11**). Likewise, the comparatively high numbers of established alien species observed for Europe and Central Asia is likely influenced by the higher availability of records for Europe and biases in the underlying database. Nonetheless, no saturation of established alien species is observed for any region (Seebens, Essl, et al., 2017).

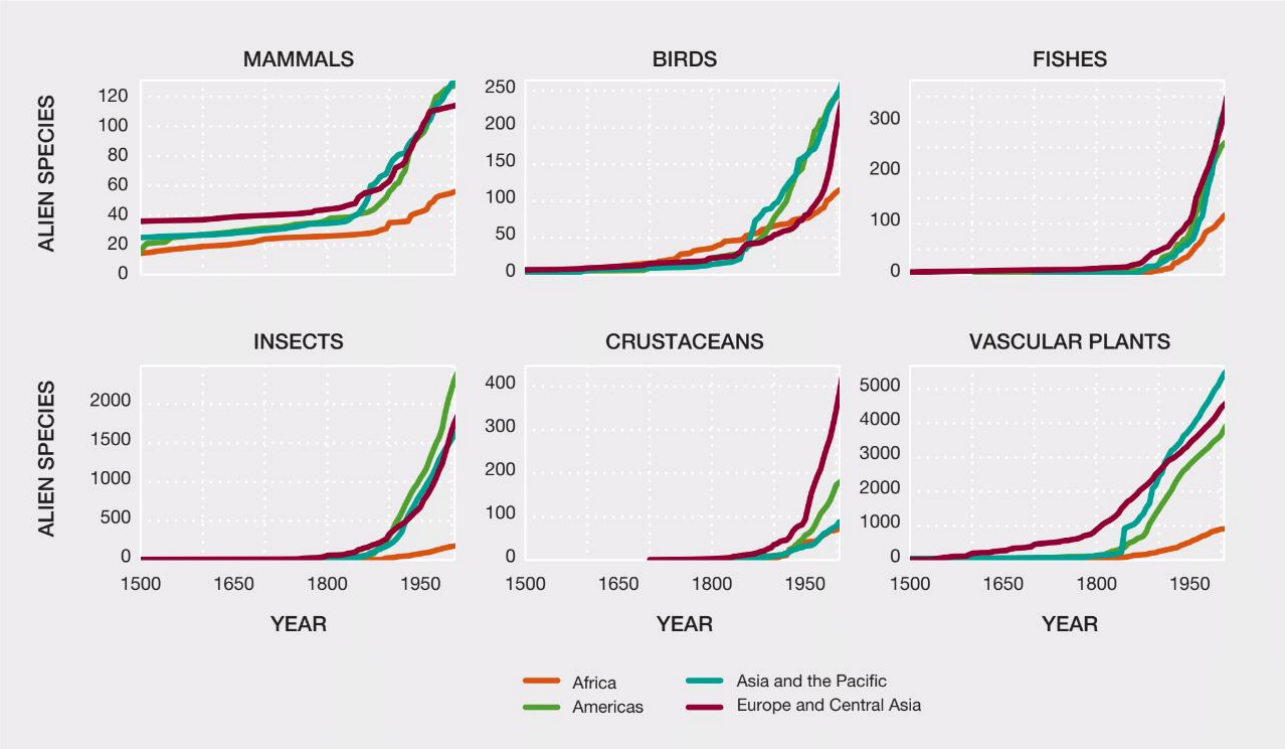

Figure 2.26. Trends in numbers of established alien species across IPBES regions. The panels show cumulative numbers of established alien species for different taxonomic groups. Numbers shown underestimate the actual extent of established alien species occurrences due to a lack of data (**section 2.1.4** for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data

management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Status

Across taxonomic groups, vascular plants provide the by far largest contribution to global established alien species numbers, followed by insects and fishes (**Table 2.19**). For many taxonomic groups, all IPBES regions except Africa report similar numbers of established alien species (**Table 2.19**). For instance, the numbers of alien vascular plant species reported for the Americas, Asia and the Pacific, Europe and Central Asia are comparable in their range, while the numbers for Africa are much lower. Similar patterns are observed for alien bird and fish species. On the other hand, algae show a different pattern with Europe and Central Asia harbouring the highest established alien species numbers, followed by the Americas, Asia and the Pacific, and Africa. However, this pattern may be influenced by variation in research intensity around the world. **Box 2.6** also presents an overview of alien and invasive alien species on land managed by Indigenous Peoples and local communities.

Table 2.19. Numbers of established alien species across IPBES regions

Numbers of established alien species can vary depending on data sources. For mammals, birds, and vascular plants, ranges of values indicate variation among databases (**section 2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this table is available at https://doi.org/10.5281/zenodo.7615582

	Africa	**Americas**	**Asia and the Pacific**	**Europe and Central Asia**	**Totals**
Mammals	30-80	83-164	97-163	72-164	197-368
Birds	121-133	249-287	287-336	221-630	495-877
Fishes	187	803	633	469	1,451
Reptiles	158	192	103	98	411
Amphibians	12	62	43	43	135
Insects	344	2,636	2,017	2,747	6,795
Arachnids	94	207	129	289	500
Molluscs	142	255	261	584	826
Crustaceans	111	213	149	451	813
Vascular plants	3,109-4,498	8,005-9,325	6,141-9,101	5,146-8,519	13,081-18,543
Algae	58	193	157	526	734
Bryophytes	0	48	32	23	88
Fungi	122	363	363	609	1,149
Oomycetes	4	12	12	59	70
Bacteria and protozoans	4	14	12	23	38
Totals	5,033-6,484	14,853-16,292	11,722-14,797	13,754-17,628	26,783-32,798

Box 2.4. Protected areas: A global assessment of trends and status of alien and invasive alien species

Protected areas around the world are crucial for preserving and sustaining biodiversity, ecosystem processes and human well-being (Gaston et al., 2008; Naughton-Treves et al., 2005). Increasingly, these areas are being threatened by numerous drivers of change in nature that are challenging the

effective management of over 200 thousand protected areas globally (Osipova et al., 2017; UNEP-WCMC et al., 2021). Biological invasions constitute a major threat to protected areas (Goodman, 2003; Osipova et al., 2017; Pyšek, Hulme, et al., 2020; Schulze et al., 2018), a concern that dates back to the 1860s (Foxcroft et al., 2017).

Seminal work on invasions in terrestrial protected areas carried out during the Scientific Committee on Problems of the Environment (SCOPE) project in the 1980s found that all 24 studied terrestrial protected areas faced challenges from invasive alien species and that invasions were not only an issue within disturbed sites (Mooney et al., 2005; Usher, 1988), but also in relatively undisturbed nature reserves. The SCOPE report also found that islands faced higher threats than mainland areas, that there was an inverse relationship between protected area size and the number of introduced species in arid land and chaparral biomes, and that there was positive correlation between number of human visitors and the presence of invasive alien species (Usher, 1988). In a study that revisited 21 of the originally studied protected areas and compared how the status of biological invasions has changed over the last 30 years, Shackleton et al. (2020) found that of all the taxa analyzed, invasive plants pose the greatest continued threat, and their numbers have increased in 31 per cent of the protected areas. Mammal invasions now represent a lesser threat due to effective management in many protected areas, with fewer invasive alien mammals now listed in 43per cent of protected areas. Invasions by amphibians, reptiles, and fish have remained fairly stable over the past three decades (R. T. Shackleton, Foxcroft, et al., 2020). The limited number of study sites included were biased towards mainland United States and Africa making regional comparisons and trends hard to meaningfully assess. More comprehensive global assessments using similar methods would address a major knowledge gap and better evaluate status and change globally providing important information for international policy (**Glossary**) mandates.

The subsequent uptake of coordinated global academic projects on protected areas has been limited, particularly for marine systems leaving many knowledge gaps on the status of invasive alien species in protected areas and the broad-scale status trends. According to Shackelton et al. (2020) there is a lack of data on freshwater invertebrates, marine species, and other taxa creating a taxonomic bias in invasion science. However, some review and synthesis work (e.g., Foxcroft et al., 2013, 2017; X. Liu et al., 2020; R. T. Shackleton, Bertzky, et al., 2020; R. T. Shackleton, Foxcroft, et al., 2020; see above) has strengthened information on the current status and key trends of invasive alien species in protected areas globally, but each effort has limitations and greater coordination on taxa and management is needed.

In “Plant invasion in Protected Areas”, Foxcroft et al. (2013) identified and illustrated key impacts of invasive alien species and outlined some mechanisms of invasion in protected areas and contributed to assessing management interventions, helping to synthesize and outline both the status of invasive alien species in protected areas and key knowledge gaps. Drawing on 14 case studies from around the world that included information from over 135 protected areas globally, the authors detailed assessments and baseline information and elucidated regional patterns and threats. One surprising result was that while intentional introductions of invasive alien species into protected areas have been assumed to be low, this is not the case. This point is further supported by Foxcroft et al. (2008) and Toral-Granda et al. (2017). Authors show that even Arctic regions now face challenges from invasive alien species (Shaw, 2013). Very few protected areas globally have good baseline information and only a handful of well-studied protected areas have robust invasive alien species lists available. Regionally there are also large differences in monitoring and information. The United States, Oceania, and some parts of Europe have more information than other regions. For example, J. A. Allen et al. (2009) highlight that there are over 7.3 million ha of invasions in 218 protected areas in the United States, with over 20,300 distinct invasion clusters by over 3,750 invasive alien species. In Central and Western Europe, Braun et al. (2016) collected and collated data on 53 invasive plant species in 46 large, protected areas finding that in 86 per cent of protected areas at least one of the 46 target invasive plants was present, and that 80 per cent of

protected areas did conduct some form of management. The mean number of invasive plants was 11.2 per protected area, however, most of them only managed a mean 4.3 species accounting for around 3 per cent of park budgets. Interestingly, park size and age had no effect on invasive alien species presence or management.

A review on plant invasion science research in protected areas (Foxcroft et al., 2017) yielded some important information on trends and status highlighting key advances in invasion science in protected areas, important policies starting with the Convention Relative to the Preservation of Fauna and Flora in their Natural State in 1933, the twelfth meeting of the Conference of the Contracting Parties to the Ramsar Convention on Wetlands in 2015, and 13 other important policy support mechanisms in-between. This review also identified 59 of the most common invasive plants in protected areas: eight species (*Arundo donax* (giant reed), *Pontederia crassipes* (water hyacinth), *Lantana camara* (lantana), *Melia azedarach* (Chinaberry), *Poa annua* (annual meadowgrass), *Psidium guajava* (guava), *Robinia pseudoacacia* (black locust), and *Rumex acetosella* (sheep's sorrel)) occur in more than 150 protected areas globally. The review showed that North America and Europe dominate work on plant invasions in protected areas globally, followed by Africa and Oceania, with very limited knowledge from other world regions, particularly in South America and Asia.

More recently, key syntheses have assessed the trends and status of invasions in terrestrial and inland waters protected areas globally (e.g., X. Liu et al., 2020; R. T. Shackleton, Bertzky, et al., 2020). X. Liu et al. (2020) assessed the establishment of 894 terrestrial alien vertebrates and invertebrates in almost 200 thousand protected areas globally and found that very few (over 10 per cent) of protected areas harbour established alien animals, but the majority (89–99 per cent) have an established population of at least one alien animal species within 10-100 km from their borders. There are 520 alien animal species in protected areas globally, the most common being birds (4.7 per cent of the protected areas, 252 species), followed by mammals (3.7 per cent, 91 species), invertebrates (2.2 per cent, 63 species), amphibians (0.5 per cent, 48 species) and reptiles (0.4 per cent, 66 species) (X. Liu et al., 2020). X. Liu et al. (2020) highlight that larger protected areas, those more recently inscribed, and those with a higher protection status were surprisingly more prone to a higher richness of alien animals. Furthermore, X. Liu et al. (2020) found that globally, protected areas in some regions and biomes are more at risk from alien animals, including birds, mammals, invertebrates, amphibian and reptiles; particularly in (sub)tropical Pacific and Caribbean Islands and New Zealand, as well as temperate mixed forests, savannas, and grasslands in the United States, western Europe, and Australia. Additionally, X. Liu et al. (2020) highlight that Africa and Asia are most often donors of alien animal species with North America and Europe being key recipient areas (**Figure 2.27**).

Shackleton, Bertzky, et al. (2020) assessed the status of biological invasions and their management in 241 natural and mixed World Heritage Sites globally and found that just over half (53 per cent) were explicitely or implicitly reported to be threatened by invasive alien species through formal IUCN/ United Nations Educational, Scientific, and Cultural Organization (UNESCO) monitoring initiatives. It is suspected that this number is much higher. Almost 300 different invasive alien species were reported to be invading World Heritage Sites. However, detailed information through UNESCO and IUCN monitoring programmes yielded limited and inconstant information so broad-scale trends were hard to assess. To overcome this a seven-step monitoring and reporting framework was developed to better collate data moving forward. This includes: (i) evaluating pathways, (ii) compiling inventories of species, (iii) identifying current impacts, (iv) reporting on management, (v) predicting future threats and management needs, (vi) identifying knowledge gaps, and (vii) assigning an overall threat level. This framework could easily be used in all categories of protected areas and could be a priority moving forward to improve monitoring and understanding.

Marine protected areas "*....as oases of biodiversity, serve as the last rampart against these invasive alien species*" (Francour et al., 2010). Alas, this is a wishful premise and biological invasions are having a large impact on marine protected areas worldwide. Large-scale global syntheses on the topic of marine invasions and protected areas are lacking, however, research on certain areas and species has provided important insights which are summarized here. Generally, European oceans and seas, as well as northern Atlantic and Pacific oceans, are most at threat from marine invasive alien species (M. J. Costello et al., 2021). More specifically, 53 marine alien species, nearly all newly reported or newly recognized as introduced, were recently documented in the Galápagos Marine Reserve, which is a large, biologically diverse and remote protected area (Carlton et al., 2019). Surveys of rocky reef fish assemblages conducted since 2000 in Mediterranean marine protected areas showed no differences in invasive fish density and biomass as compared to adjacent unprotected areas. In the south and eastern Mediterranean Sea invasive alien species have higher species richness and biomass as compared to local fish biota (D'Amen & Azzurro, 2020; Galil, 2017; Giakoumi et al., 2019; Guidetti et al., 2014). Indeed, a recent assessment in protected areas along the Mediterranean coast of Turkey identified 289 alien vertebrates, invertebrates and algae (Bilecenoğlu & Çınar, 2021). The reduction of protected areas to nursery sites for certain invasive alien species is most acute in the South-eastern Mediterranean but occurs throughout the sea and in the adjacent Atlantic (Blanco et al., 2020; Cacabelos et al., 2020; Mazaris & Katsanevakis, 2018; Wangensteen et al., 2018). From a species point of view, the spread of the venomous Indo-Pacific lionfish, *Pterois volitans* (red lionfish) and *Pterois miles* (lionfish), across the tropical western Atlantic and the Caribbean Sea was swift, not sparing marine protected areas, including large, established, well-cared for and remote ones (e.g., Florida Keys National Marine Sanctuary, United States; Flower Garden Banks National Marine Sanctuary, United States; The Parque Nacional Arrecife Alacranes, Mexico) (Johnston et al., 2013; López-Gómez et al., 2014; Ruttenberg et al., 2012), illustrating the threat that invasive marine species pose to conservation. Poor management and the lack of effective policies have been nullifying conservation goals in marine protected areas in regions exposed to biological invasions (Bilecenoğlu & Çınar, 2021; B. Galil, 2017; Mazaris & Katsanevakis, 2018; **Chapters 5** and **6**).

Foxcroft et al. (2017) mention three key needs to better understand the current status of biological invasions and their management in protected areas globally and to better assess key trends. These include (i) establish a global working group to better coordinate research, (ii) develop standardized protocols and tools for large-scale and long-term monitoring of invasive alien species in protected areas globally, and (iii) better account for and respond to different socioecological contexts in research and management. Importantly, many regions of the world have limited baseline and empirical evidence concerning biological invasions and their management making this fundamental research crucial. The collection of baseline data is increasingly being conducted in data poor areas (e.g., Bhatta et al., 2020; Foxcroft et al., 2017; Padmanaba et al., 2017), but more is needed. Furthermore, improved monitoring and assessment globally is important to answer long-standing and disputed questions relating to invasions in protected areas. For example, whether or not protected areas impose biotic resistance (**Glossary**) against invasions (Meiners & Pickett, 2013). Some evidence suggests protected areas act as a barrier, or refuge, against invasions (Ackerman et al., 2017; Foxcroft, Jarošík, et al., 2010; Gallardo et al., 2017), but other studies show the contrary (Byers, 2005; Holenstein et al., 2021; Klinger et al., 2006). Further work drawing on a multitude of taxa in different socioecological systems is needed to fully understand the role of protected areas in invasions, which is likely to differ by taxa and environmental settings.

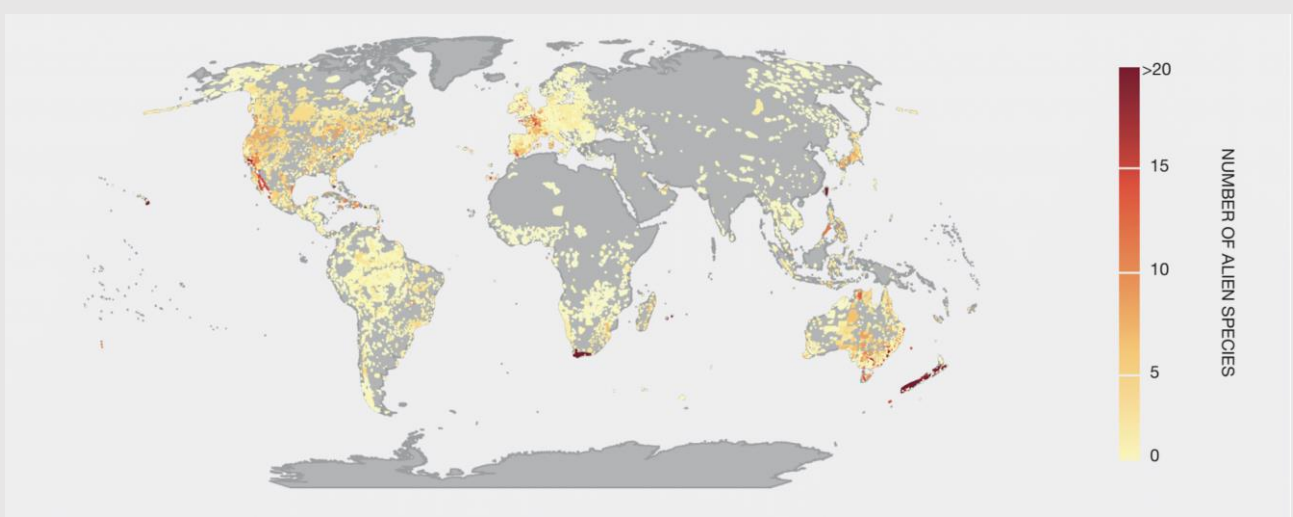

Figure 2.27. Numbers of established alien vertebrate species per terrestrial protected area. Among the top 50 protected areas, 32 per cent are located in New Zealand, 26 per cent in Taiwan, Province of China, 16 per cent in the United States (mostly on Hawaii), 12 per cent in Great Britain and 6 per cent on Réunion. Adapted from X. Liu et al. (2020), https://doi.org/10.1038/s41467-020-16719-2, under license CC BY 4.0.

Box 2.5. **Islands: A global assessment of trends and status of alien and invasive alien species**

One-quarter of the countries in the world are islands or groups of islands, and over two-thirds of all countries include islands (Russell & Kueffer, 2019). Taken together, the Earth's islands represent 5.3 per cent of the total land surface (Global Islands Network, 2021; Tershy et al., 2015). Because of their very high rates of endemism (9.5 and 8.1 times higher than continents for vascular plants and vertebrates, respectively), and with over 20 per cent of the world's terrestrial species, islands are considered centres of biodiversity (Kier et al., 2009). As a result, 10 of the 35 world's biodiversity hotspots (i.e., regions where biodiversity is both the richest and the most threatened (Mittermeier et al., 2011) are entirely, or largely consist of, islands (Bellard et al., 2014). Globally, islands represent concentrated regions of biodiversity loss in the past and present, and this trend is predicted to continue in the future (Russell & Kueffer, 2019; Whittaker & Fernández-Palacios, 2006).

Islands harbour some of the highest numbers of established alien species (Dawson et al., 2017; Essl et al., 2019), particularly small and remote tropical and sub-tropical islands with high numbers of invasive alien plants per unit of surface (Pyšek, Pergl, et al., 2017), a pattern that holds across taxonomic groups (Moser et al., 2018; Turbelin et al., 2017). This is especially acute in former European island colonies with long histories of repeated species introductions (Turbelin et al., 2017). Furthermore, nearly 50 per cent of all species at risk (**Glossary**) of extinction on the IUCN Red List are found on islands and species on islands are more likely to be threatened by biological invasions (almost three-quarters of threatened species; Leclerc et al., 2018). While all threats interact on islands to cause declines in native species abundance, biological invasions consistently lead to the extinction of insular populations, particularly through predation and disease (Russell & Kueffer, 2019; **Chapter 4**, **section 4.3.1.1**). However, particularly independent small island developing states (SIDS) and island territories with dependencies on larger continental economies (Blackburn et al., 2016; Meyerson & Reaser, 2003; Reaser & Meyerson, 2003; Russell et al., 2017) have few resources for invasive alien species research, management, cooperation, and capacity-building (Reaser & Meyerson, 2003; Veitch et al., 2019).

Trends

Temporal trends of biological invasions on islands can be classified into three distinct periods with contrasting dynamics; first contact (Indigenous Peoples and local communities), modern history (1500), and the contemporary twentieth century onwards era (Keppel et al., 2014; Russell & Kueffer, 2019; **Figure 2.28**). In the first period, island syndromes (Wroe et al., 2006) and the lack of refugia on small islands made insular species more vulnerable to biological invasions than continental species (Wroe et al., 2006). The second period corresponds to the "Age of Discovery", the timing of which in different parts of the world coincided with colonization of islands by Europeans (Russell & Kueffer, 2019). During this period, unintentional and intentional (and sometimes repeated) introductions of many animals and plants were facilitated by the establishment of regular shipping lines (Seebens et al., 2013). This led to successful invasions by a large number of species on many islands of various ecosystem types (Russell & Kueffer, 2019). The third period is associated with globalization that included a distinct increase in world trade, migration, and tourism, all of which affected islands worldwide. The emergence and rise of rapid international transit increased substantially both the diversity of introduction vectors and pathways (Hulme, 2009, 2021; Meyerson & Mooney, 2007), and the associated number of these introductions (van Kleunen et al., 2015). The number, frequency, and geographic origin of biological invasions to and among islands also increased with time, following the growth of human populations on these islands (both residents and tourists), as exemplified by the Galapagos (Toral-Granda et al., 2017). At the same time, awareness was rising, and more research was underway to detect and report new species. Other important predictors for established alien species on islands are the existence of military bases or paved airfields (Denslow et al., 2009).

Most introduced species on islands today only occupy a small portion of their final predicted range and are thus likely to expand further (M. J. B. Dyer et al., 2018; Trueman et al., 2010). In addition, more species from both the existing pool of alien species and those species not currently introduced outside their native range will continue to colonize and establish on islands in the future (Bellard et al., 2017). Islands are also disproportionately vulnerable to climate change which may increase the rate of establishment and spread of many invasive alien species on islands (X. Li et al., 2020). More frequent climate-induced disturbances (e.g., flooding, treefall, and landslides caused by tropical cyclones) and/or droughts increase the invasibility of native ecosystems affecting, for instance, the structure of island forests (Boehmer, 2011; Ehbrecht et al., 2021; Pouteau & Birnbaum, 2016; Wyse et al., 2018).

The accumulation rate of established alien species on islands is not slowing and the future invasive alien species will differ in type from species that have invaded islands in the past. These emerging invasive alien species include groups such as microorganisms and pathogens, as well as reptiles from the pet trade (Apanius et al., 2000; Russell & Kueffer, 2019), which will likely lead to new species interactions with both direct and indirect ecological consequences (Forey et al., 2021; J.-Y. Meyer et al., 2021). In the future, the vectors and pathways of biological invasions are predicted to further evolve and to keep interacting with other drivers of change in nature, such as climate change (Russell et al., 2017), and will continue to be of great concern for biodiversity conservation (Lenzner et al., 2020; S. Taylor & Kumar, 2016). For instance, climate-induced forest decline is likely to increase the vulnerability of Pacific Island rainforests to invasive alien plants (Boehmer, 2011; Mertelmeyer et al., 2019) and facilitate invasional meltdowns (Minden et al., 2010).

Status

Most islands are affected by biological invasions with insular ecosystems being the recipients of 80 per cent of documented bird and mammal introductions (Ebenhard, 1988). At least 65 major island groups have been invaded by *Felis catus* (cat) (Atkinson, 1989) and over 80 per cent of all major island groups have also been invaded by *Rattus* spp. (rat) (Atkinson, 1985). If plants and invertebrates are included in assessments, biodiversity is most severely affected by biological invasions in the Pacific and Atlantic insular regions (Leclerc et al., 2018). For plants, 26 per cent

(82 islands) of islands covered in the GloNAF database harbour more established alien than native species (Essl et al., 2019). The identity of invasive alien species and their impacts differ by region, island type, and associated ecosystems, but the cumulative pattern of impacts is consistent across world regions (Leclerc et al., 2020).

Across SIDS, 8,668 presence records for 2,034 potential invasive alien species have been registered, 76 per cent of which are plants, 23 per cent animals, and 1 per cent fungi, chromists, viruses, bacteria, and protozoa (Russell et al., 2017). Over half (53 per cent) of these species were identified as invasive alien species on at least one SIDS, while information was often lacking for the remaining species (Lenz et al., 2021). Long-distance transportation by ship and plane dominates invasive alien species pathways to islands, distinguishing islands from continents and natural colonization in rate and type (Hulme et al., 2008), such as for *Anolis* spp. (anole lizards) on Caribbean islands (Helmus et al., 2014). Only one study has focused on plant invasions in urban environments of SIDS (Lowry et al., 2020). Given rapid changes expected in Pacific country urban areas in coming decades, it is a critical to fill this gap (ADB, 2012).

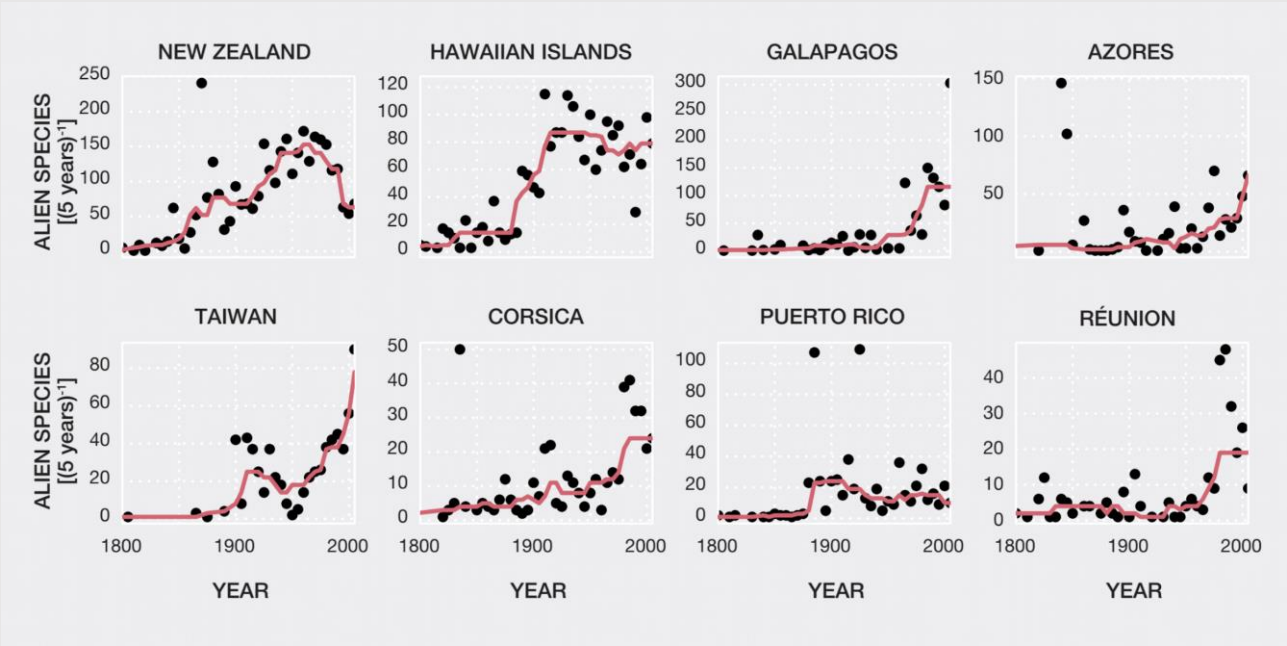

Figure 2.28. Trends in numbers of established alien species for selected islands. The panels show numbers of established alien species per five-year intervals for those islands with the highest numbers of recorded established alien species. Numbers shown underestimate the actual extent of alien species occurrences due to a lack of data. Smoothed trends (lines) are calculated as running medians (**section 2.1.4** for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Box 2.6. Land managed, used or owned by Indigenous Peoples and local communities: A global assessment of trends and status of alien and invasive alien species

Indigenous Peoples and local communities (i.e., typically ethnic groups who are descended from and identify with the original inhabitants of a given region) manage or have tenure rights over a large area of land. For Indigenous Peoples only, it is estimated that they manage or have tenure rights for at least 28 per cent of the total land area worldwide (Garnett et al., 2018). Their land

(hereafter called "Indigenous lands") intersects with 40 per cent of the world's protected areas and hosts higher amounts of natural areas compared to other lands (Garnett et al., 2018). Although Indigenous lands are often less inhabited and more remote than other lands, they do not escape anthropogenic pressures. It is unsurprising to find many alien and invasive alien species on lands managed by Indigenous Peoples and local communities and indeed has been frequently reported from such lands all over the world (Gautam et al., 2013; Kannan et al., 2016; Ksenofontov et al., 2019; Miranda-Chumacero et al., 2012; Thorn, 2019). To date, no study has investigated the distribution of alien and invasive alien species on Indigenous lands.

The following analysis was conducted to deepen the understanding about the distribution of alien and invasive alien species on Indigenous land. As described in **section 2.1.4**, occurrences of populations of more than 17,000 established alien species worldwide were obtained using occurrence records provided by GBIF and the Ocean Biodiversity Information System (OBIS). These point-wise occurrences were integrated with a spatial layer of land managed, used or owned by Indigenous Peoples (Garnett et al., 2018) to determine the total number of established alien and invasive alien species recorded on Indigenous lands.

This analysis revealed that, in total, 6,351 established alien species have been recorded on Indigenous lands, which is 34 per cent of all established alien species recorded worldwide in this data set. The number of invasive alien species according to the GRIIS database (Pagad et al., 2022) amounts to 2,355 (56 per cent of the total number globally) on these lands, although it could not be determined whether the invasive alien species pose any impact on these lands (see **Chapter 4, section 4.6** for a detailed assessment of impacts by Indigenous Peoples and local communities). The number of established alien species recorded on Indigenous lands is highly correlated with the total number of established alien species of the same country (t-test: $t=12.8$, $df=77$, $p<0.001$, $r=0.82$). That is, in countries with high numbers of established alien species, those numbers are also high on Indigenous lands. However, the number of established alien species recorded on Indigenous land is on average consistently lower compared to those numbers recorded on other lands also after taking area into account (**Figure 2.29**). Hotspots of occurrences with high established alien species numbers on Indigenous lands were found all over the world but particularly in Australia (2,624 alien species), United States (1,719), Mexico (746), Sweden (690) and Russia (650). The same sequence applies to invasive alien species numbers, although at a lower magnitude: Australia (1,172 invasive alien species), United States (691), Mexico (481), Sweden (441), and Russia (436) (**Figure 2.29**).

An analysis of the trends of alien and invasive alien species on Indigenous lands is currently missing due to a lack of data, but it seems very likely that the number of established alien species on Indigenous lands increased as observed for other regions (**Figures 2.4** and **2.26**) and so are the impacts they cause. A clear knowledge gap exists for information about the trends and status of invasive alien species in coastal waters managed by Indigenous Peoples and local communities.

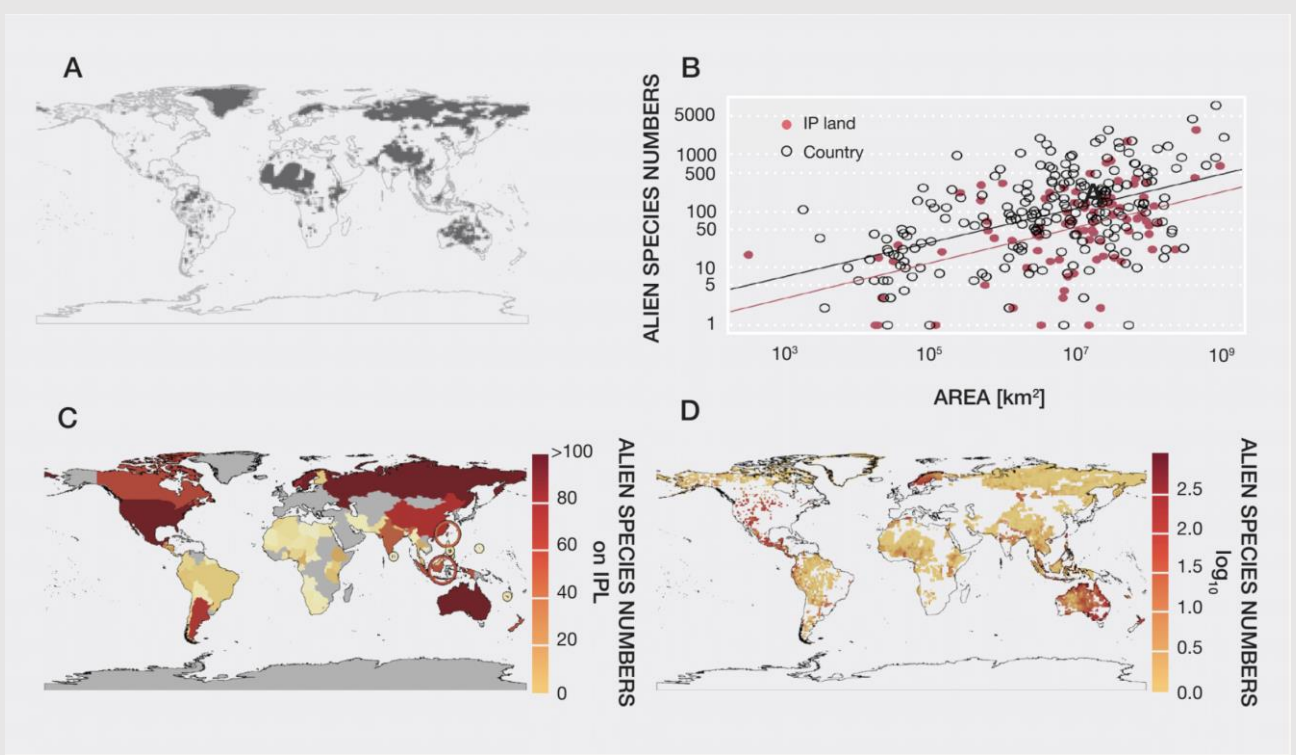

Figure 2.29. Invasive alien species on Indigenous People's land. (A) Land managed, used or owned by Indigenous Peoples. (B) Species-area relationships for established alien species per country (circles) and per area of Indigenous lands (IP) lands (dots), showing a consistently lower number of established alien species on Indigenous lands. (C) Number of alien species on Indigenous lands per country. (D) Number of established alien species on Indigenous lands per grid cell. A data management report for this figure is available at https://doi.org/10.5281/zenodo.7615582

2.4.2. Trends and status of alien and invasive alien species in Africa

This section reports on the trends and status of established alien species of Africa for animals (**section 2.4.2.1**), plants (**section 2.4.2.2**), microorganisms (**section 2.4.2.3**), and islands (**section 2.4.2.4**), and provides an overview of data and knowledge gaps (**section 2.4.2.5**). A description of IPBES regions and sub-regions including a spatial representation is provided online (IPBES Technical Support Unit On Knowledge And Data, 2021) and in **Chapter 1**, **section 1.6.4**.

2.4.2.1. Animals

Trends

The first alien mammal species to arrive in Africa were probably domesticated bovids, pigs, cats, and dogs during the spread of agriculture, followed by commensal rodents, mostly limited at present to anthropized and densely populated areas (Long, 2003). Other introductions took place on the western coast of North Africa where *Mustela nivalis* (weasel) was likely a rodent biocontrol agent, *Apodemus sylvaticus* (long-tailed field mouse), a stowaway, and *Bubalus bubalis* (Asian water buffalo) livestock. More introductions began in the twelfth century such as *Suncus murinus* (Asian house shrew) as a stowaway. A rapid increase of mammal introductions during the nineteenth and twentieth centuries was mainly due to hunting, ecotourism, and the pet trade pathways (Biancolini et al., 2021). Acclimatization societies were very active in South Africa and carried out numerous bird and mammal introductions to "improve" the aesthetic of the South-African landscape from a European point of view after the mid-1800s (B. W. van Wilgen et al., 2020). In the last century, increasing global trade combined with the advent of the game-farming

industry and ecotourism resulted in a striking rise in introductions of alien vertebrates and invertebrates (Picker & Griffiths, 2017; B. W. van Wilgen et al., 2020).

As for other taxa, African regions with the earliest records of established alien species tend to have higher numbers of established alien species. For fishes, particularly high numbers of established alien species were recorded in North Africa due to Lessepsian invasion of marine species through the Suez Canal and to its closer socio-economic relationship with Europe (**Figure 2.30**). Indeed, the number of alien fish in North Africa accelerated markedly after 1869 when the Suez Canal opened (Galil, 2000). In South Africa an increasing trend in established alien species detections is indicated as the number of marine alien species reported has increased from 15 (Griffiths et al., 1992) to 95 established alien species (T. B. Robinson et al., 2020). Although there is no doubt that new species are being introduced, other factors are also contributing to the increase in introductions, such as deeper historical analyses of past introductions (Mead et al., 2011), varying levels of available taxonomic expertise across time (Griffiths et al., 2009), and increased research efforts on underrepresented taxa or in under-studied ecosystems (T. B. Robinson et al., 2020).

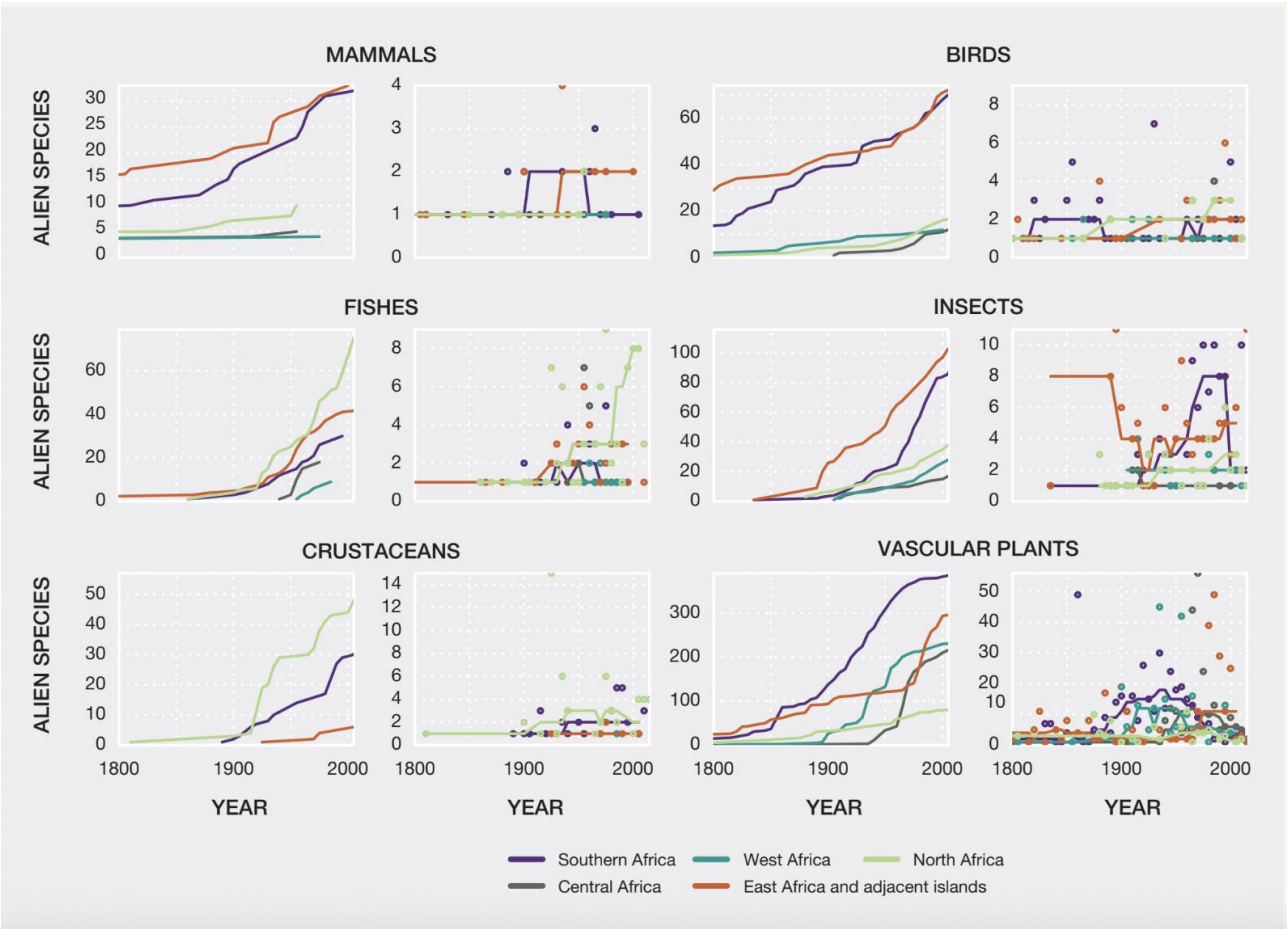

Figure 2.30. Trends in numbers of established alien species for Africa. Panels show cumulative numbers (left panels) and numbers of established alien species per five-year intervals (right panels). Numbers here underestimate the actual extent of established alien species occurrences due to a lack of data. Lines in right panels indicate smoothed trends calculated as running medians (**section 2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

With the exception of plants, the introduction of alien species into freshwater systems in Africa has largely been intentional to enhance ecosystem services and promote nutritional, economic, or recreational values (Gherardi, Britton, et al., 2011; Howard & Chege, 2007; Howard & Matindi,

2003; Munyaradzi & Mohamed-Katerere, 2006; Weyl et al., 2020). However, the outcomes of these introductions were often opposite of the intended purpose, with losses of ecosystem function and services (B. W. van Wilgen et al., 2020). For example, in South Africa the overall rate of alien freshwater animal introductions accelerated sharply after 1880 and generally increased over time, with unintentional introductions of invertebrates playing a relevant role (Weyl et al., 2020). Only freshwater fish introductions underwent a significant decrease after the 1950s due to legislation regulating introductions and decreasing demand for new species for angling (Faulkner et al., 2020). In general, the number of invertebrate introductions to South Africa rose over time (Faulkner et al., 2016), this pattern being reported for freshwater (Weyl et al., 2020), terrestrial (Janion-Scheepers & Griffiths, 2020), and marine invertebrate introductions (T. B. Robinson et al., 2020).

Status

In light of Africa's colonial history, there have been surprisingly fewer introductions of alien mammals than to other regions (Long, 2003). Africa currently harbours 44 established alien mammals from seven orders and 18 families (Biancolini et al., 2021). The most represented orders are Cetartiodactyla (17 species), Primates (9), Rodentia (7), and Carnivora (6). These alien species are mainly concentrated along the western Mediterranean coast, South Africa, and Madagascar and originate from within Africa (16), Europe and Central Asia (8), the Americas (8), and Asia and the Pacific (1). The pathways most frequently involved in alien mammal establishment were hunting (15 cases), the pet trade (10), farming (8), and conservation (8) (Biancolini et al., 2021). Escaped game species are a growing problem in South Africa where numerous game-farming estates specialize in alien mammals (D. Spear & Chown, 2009; B. W. van Wilgen et al., 2020). The status of these species is often classified as "within country" instead of alien as they are native to the geopolitical unit of South Africa. Nevertheless, they have been translocated outside of their historical native range (B. W. van Wilgen et al., 2020). For example, *Tragelaphus angasii* (nyala), an antelope native to Africa, is now spreading outside its native range and possibly competing with native herbivores (Biancolini et al., 2021; Downs & Coates, 2005). Of the 44 established alien mammal species, 27 (61.4 per cent) have ecological impacts (Biancolini et al., 2021). For example, *Suncus murinus* (Asian house shrew), one of the "100 of the worst invasive alien species," has a patchy distribution from Madagascar to Egypt, and potentially has overlooked impacts on native plants, invertebrates, and small vertebrates through predation or competition (GISD, 2019). However, some alien mammal introductions were considered benign and carried out for conservation, such as for four primates threatened by habitat loss and translocated from their native mainland range to insular protected areas: *Daubentonia madagascariensis* (aye-aye), *Eulemur albifrons* (white-headed lemur), *Varecia variegata* (black-and-white ruffed lemur), and *Piliocolobus kirkii* (Zanzibar red colobus) (Andriaholinirina, Baden, Blanco, Chikhi, Cooke, et al., 2014; Andriaholinirina, Baden, Blanco, Chikhi, Zaramody, et al., 2014a, 2014b; Biancolini et al., 2021; Davenport et al., 2019).

Most alien bird species in Africa are found in the far south of the continent, although *Corvus splendens* (house crow) is distributed from Sudan to South Africa along the east coast. Most alien species are a legacy of Africa's European colonial past, such as *Fringilla coelebs* (chaffinch) and *Sturnus vulgaris* (common starling) in South Africa. Other notable alien birds in Africa are *Acridotheres tristis* (common myna) and *Passer domesticus* (house sparrow) (E. E. Dyer, Redding, et al., 2017).

The number of alien reptile introductions in Southern Africa has risen in recent decades, but there is limited information about the trends elsewhere in this IPBES region (Capinha et al., 2017; Kraus, 2009; Seebens, Blackburn, et al., 2017; Van Wilgen et al., 2010). For amphibians, many species have been translocated within Southern Africa (Measey et al., 2017).

In contrast to most other taxa, the highest numbers of alien fishes and crustaceans – many marine – are found in North Africa (**Table 2.19**). East Africa and its adjacent islands have the second highest numbers of alien fishes likely because of introductions in the many lakes of the Rift Valley area, including the three largest, Lakes Victoria, Tanganyika, and Malawi, that have high alien fish population densities and associated fisheries important for subsistence (Pitcher & Hart, 1995). In these lakes and large artificial reservoirs, *Lates niloticus* (Nile perch), *Limnothrissa miodon* (Tanganyika sardine), and tilapias are the main introduced fish species (Craig, 1992; Pitcher & Hart, 1995). Tilapias are tropical fishes in the family Cichlidae (mainly *Oreochromis*, *Tilapia*, and *Sarotherodon* spp.) that are native to parts of Africa and the Middle East but have been introduced globally mostly for aquaculture and human consumption (Canonico et al., 2005). A total of 21 alien freshwater fishes have established in South Africa, and others have been translocated (Ellender & Weyl, 2014; Weyl et al., 2020). The high number of alien fishes in Southern Africa is likely influenced by greater research efforts compared to other African regions. No alien marine fish have been reported for South Africa yet (T. B. Robinson et al., 2020). Many freshwater fish have been intentionally introduced across Africa in order to maintain or increase fishery yields, enhance sport fisheries, or support the aquaculture industry (Darwall et al., 2011; Ellender & Weyl, 2014; García et al., 2010; Máiz-Tomé et al., 2018). By 2011, sixteen alien fish species had been introduced to Central Africa (Brooks et al., 2011). In Madagascar, one quarter of the freshwater fish fauna consists of alien species, with 26 alien species present, of which at least 24 were deliberately introduced during the 1950s (Šimková et al., 2019). On Île de la Réunion, six species of fish (and one decapod crustacean, *Macrobrachium rosenbergii* (giant freshwater prawn)) were introduced by 2002, but only four were established by then (Keith, 2002).

Notably, no review on introductions of freshwater alien species in Africa has been produced so far except for crayfish (Madzivanzira et al., 2021). In other cases, current information is available only for specific taxa and has been only comprehensively and recently assessed for South Africa (M. P. Hill et al., 2020; Weyl et al., 2020; Zengeya & Wilson, 2020). Available data show that South Africa hosts 51 alien freshwater invertebrates and 32 alien freshwater fish, while 926 alien plant species are reported, and freshwater and terrestrial species are not distinguished (Zengeya & Wilson, 2020). Seventy-seven alien freshwater animals, largely dominated by fishes, molluscs, and crustaceans, are currently established in South Africa, most of which were intentionally introduced (Picker & Griffiths, 2017; Weyl et al., 2020).

Among alien freshwater jellyfish, the cnidarian *Craspedacusta sowerbii* (peach blossom jellyfish) has been recorded in South Africa and potentially Morocco (Oualid et al., 2019; Weyl et al., 2020). Several species of alien molluscs have been recorded in African freshwaters, with 14 species of gastropods reported by 2011, some of which were released for the biological control of the intermediate hosts of schistosomiasis (Appleton, 2003; Appleton & Brackenbury, 1998). Only one alien freshwater bivalve *Corbicula fluminea* (Asian clam) has been recorded in African waters, an introduction probably related to fish stocking (Clavero et al., 2012; Darwall et al., 2011). Nine species of alien crayfish have been introduced to Africa, mostly for aquaculture. Five have established populations in the wild and three have spread widely in specific parts of Africa: *Procambarus clarkii* (red swamp crayfish) in Eastern Africa, *Cherax quadricarinatus* (redclaw crayfish) in Southern Africa, and *Procambarus virginalis* (Marmorkrebs) in Madagascar (Madzivanzira et al., 2021).

Little is known about marine alien species in Africa. The most studied areas are along the South African coast which includes two large marine ecosystems, the Agulhas current in the east and the Benguela current in the west (Mead et al., 2011; T. B. Robinson et al., 2020). The total number of introduced marine species reported is 95, with 59 per cent considered as invasive alien species. A variety of taxa are represented, from the small protists (e.g., *Mirofolliculina limnoriae*) and dinoflagellates (e.g., *Alexandrium minutum*) to the most conspicuous macroalgae, molluscs, crustaceans, bryozoans, and tunicates. Most biological invasions were reported along the Benguela

current large marine ecosystem (70 per cent) and alien species inhabit bays, estuaries, and artificial habitats, while only three are widespread and abundant on open rocky shores (the mussels *Mytilus galloprovincialis* (Mediterranean mussel) and *Semimytilus patagonicus*, and the barnacle *Balanus glandula*) (T. B. Robinson et al., 2020). Angola harbours 29 introduced marine species, mostly concentrated in Luanda, the most studied area of the country (Pestana et al., 2017). The most conspicuous and abundant taxa are bryozoans and tunicates, such as *Schizoporella errata* (branching bryozoan) and *Ascidiella aspersa* (European sea squirt), both global invasive alien species.

2.4.2.2. Plants

Trends

The number of established alien plant species in Africa has continually increased for centuries as reported for multiple African countries (Brundu & Camarda, 2013; L. Henderson, 2006; Maroyi, 2012; Senan et al., 2012; Shaltout et al., 2016). Southern Africa has experienced a steady increase in plant alien species numbers during the entire twentieth century, the most rapid rise of all African regions, and appeared to slow down only towards the end of the century (**Figure 2.30**). In contrast, alien plant numbers in East Africa showed a marked acceleration starting in the final quarter of the twentieth century and have not yet slowed. In North Africa, alien plant numbers increased slowly but steadily towards the end of the nineteenth century. No readily apparent dynamics were detected for West Africa. However, this detected pattern is, to some extent, likely due to more intensive research and better data collected for the Republic of South Africa relative to the rest of the continent (Pyšek et al., 2008; Pyšek, Pergl, van Kleunen, et al., 2020).

Status

Southern Africa has the highest established alien species richness for all taxa (1,139) among all the subregions of Africa (**Table 2.19**). Seven other countries harbour over 300 established alien plant species: Congo (522), Ethiopia (421), Morocco (410), Mozambique (396), Benin (333), Algeria (328), and Eswatini (315) (D. M. Richardson et al., 2020). Expressed as the proportional contribution of established alien species to the national flora, countries that rank highest in this respect are Chad (12 per cent), Benin (11 per cent), and Eswatini (10 per cent); in South Africa, because of its extremely rich native flora, the contribution of established alien species to the total floristic richness of the country is only 5 per cent. South Africa also has the highest number of invasive alien species (374, D. M. Richardson et al., 2020). *Bidens pilosa* (blackjack, occurring in 61 per cent of all African regions as defined by GloNAF corresponding mostly to countries), *Ricinus communis* (castor bean, 60 per cent), *Senna occidentalis* (coffee senna, 60 per cent), *Catharanthus roseus* (Madagascar periwinkle, 56 per cent), and *Euphorbia hirta* (garden spurge, 54 per cent) occur in more than half of the regions in Southern Africa. The following are the most widely distributed invasive alien plants in Southern Africa: *Lantana camara* (lantana, invasive in 46 per cent of regions), *Tithonia diversifolia* (Mexican sunflower), *Pontederia crassipes* (water hyacinth), *Chromolaena odorata* (Siam weed), *Leucaena leucocephala* (leucaena), *Prosopis juliflora* (mesquite, all invasive in more than 20 per cent of regions), and *Parthenium hysterophorus* (parthenium weed) (D. M. Richardson et al., 2020). Concerning the donor regions of established alien plant species in Africa, the highest numbers were introduced from temperate Asia (19 per cent of all introductions to individual countries), Europe (13.9 per cent), tropical Asia (13.7 per cent), Southern America (13.4 per cent), and Northern America (10.9 per cent). However, 21 per cent of species that are established in African countries were introduced from another country on that same continent (van Kleunen et al., 2015).

Alien tree species have had the greatest impact throughout Africa on biodiversity, water regimes, fire regimes, and ecosystem functioning (D. M. Richardson et al., 2021). Many tree species used in

forestry and agroforestry, especially *Eucalyptus* and *Pinus* (Pine), have been introduced throughout Africa, and some shrubs and trees such as *Acacia colei* (parta), *Acacia melanoxylon* (Australian blackwood), *Broussonetia papyrifera* (paper mulberry), *Calliandra houstoniana* (calliandra), *Calotropis gigantea* (yercum fibre), *Dahlia imperialis* (bell tree dahlia), *Ipomoea carnea* (pink morning glory), *Montanoa hibiscifolia* (tree daisy), and *Tecoma stans* (yellow bells) are well established in many parts of the continent (D. M. Richardson et al., 2021). However, relative to *Pinus* and *Acacia*, *Eucalyptus* appears to have had a lower impact. South Africa's Mediterranean shrublands have been severely invaded by numerous alien trees and shrubs, especially species in the genera *Acacia*, *Hakea*, *Leptospermum* and *Pinus* (B. W. van Wilgen et al., 2016). Australian *Acacia* species are actively promoted for agroforestry in other parts of the continent (D. M. Richardson et al., 2004) and higher-lying areas have been heavily invaded by *Acacia melanoxylon* and *Acacia mearnsii* (black wattle), *Pinus patula* (Mexican weeping pine) and *Pinus radiata* (radiata pine). Pines and acacias are extremely invasive in the mountains of southwestern South Africa and in riparian habitats and other biomes (Holmes et al., 2005). Other tree and shrub invaders with impacts include *Acacia dealbata* (acacia bernier), *Acacia decurrens* (green wattle), several *Rubus* (bramble) species, and *Biancaea decapetala* (Mysore thorn). *Azadirachta indica* (neem tree), *Prosopis juliflora* (mesquite), and *Leucaena leucocephala* (leucaena) are abundant invaders along the coastline of much of Africa, preferring hot and humid conditions. *Chromolaena odorata* (Siam weed) is now common in many countries in Central and Southern Africa, being abundant in open savanna grasslands, woodlands, riparian zones, forest gaps, and edges (D. M. Richardson et al., 2021). **Table 2.20** lists the most widespread invasive alien species in Africa according to GRIIS.

By 2006, a total of 27 major invasive alien aquatic plants had been recorded in African waters, 16 alien to Africa, and 11 native to other parts of the continent (Howard & Chege, 2007). A recent review records the existence of 19 established alien freshwater plants only in South Africa, mainly introduced through trade and hitchhiking via boating and angling (M. P. Hill et al., 2020). In South Africa, the most important invasive alien freshwater macrophyte remains *Pontederia crassipes* (water hyacinth), first recorded as established in KwaZulu-Natal in 1910. Four other species are also highly invasive, collectively referred to along with water hyacinth as the "Big Bad Five": *Pistia stratiotes* (water lettuce), *Salvinia × molesta* (kariba weed), *Myriophyllum aquaticum* (parrot's feather), and *Azolla filiculoides* (water fern) (M. P. Hill et al., 2020; **Chapter 4**, **section 4.3.2.2**).

Table 2.20. Numbers of established alien species for subregions of Africa

For mammals, birds, and vascular plants ranges of values indicate variation among databases (**section 2.1.4** for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this table is available at https://doi.org/10.5281/zenodo.7615582

	Central Africa	**East Africa and adjacent islands**	**North Africa**	**Southern Africa**	**West Africa**	**Total**
Mammals	4-17	17-35	5-17	9-54	1-9	30-80
Birds	13-16	77-79	17-20	71-74	14-23	121-133
Fishes	26	56	130	46	17	187
Reptiles	2	33	8	124	9	158
Amphibians	0	5	2	2	5	12
Insects	33	143	71	227	48	344
Arachnids	9	29	10	70	11	94

Molluscs	2	11	75	67	7	142
Crustaceans	1	11	82	47	3	125
Vascular plants	880-1,071	1,738-2,570	485-1,162	1,754-2,292	645-818	3,109-4,498
Algae	3	4	42	12	1	58
Bryophytes	0	0	0	0	0	0
Fungi	19	44	18	82	9	122
Oomycetes	0	1	0	3	0	4
Bacteria and protozoans	1	2	1	2	1	4
Total	1,045-1,252	2,274-3,126	1,115-1,807	2,773-3,359	802-992	4,510-5,961

Table 2.21. Top most widespread invasive alien species for Africa

The number of regions where the respective species has been recorded and classified as being invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien species rather than their impacts, which is covered in **Chapter 4**. A maximum of three species is shown for each group (see **section 2.1.4** for further details about data sources and data processing). A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species name	No. of regions	Species name	No. of regions
Mammals		**Molluscs**	
Rattus rattus (black rat)	7	*Lissachatina fulica* (giant African land snail)	4
Mus musculus (house mouse)	6	*Pseudosuccinea columella* (mimic lymnaea)	3
Felis catus (cat)	5	*Bursatella leachii* (blue-spotted sea hare)	2
Birds		**Crustaceans**	
Corvus splendens (house crow)	9	*Penaeus monodon* (giant tiger prawn)	4
Acridotheres tristis (common myna)	4	*Cherax quadricarinatus* (redclaw crayfish)	3
Passer domesticus (house sparrow)	3	*Percnon gibbesi* (nimble spray crab)	2
Fishes		**Vascular plants**	
Poecilia reticulata (guppy)	9	*Lantana camara* (lantana)	31
Gambusia holbrooki (eastern mosquitofish)	7	*Pontederia crassipes* (water hyacinth)	30
Oreochromis niloticus (Nile tilapia)	6	*Chromolaena odorata* (Siam weed)	23
Reptiles		**Algae**	
Trachemys scripta elegans (red-eared slider)	3	*Caulerpa cylindracea* (green algae)	2
Hemidactylus frenatus (common house gecko)	2	*Alexandrium tamarense* (dinoflagellate)	1
Gehyra mutilata (mutilating gecko)	1	*Caulerpa chemnitzia* (green algae)	1
Amphibians		**Bryophytes**	
Rhinella marina (cane toad)	2		

Duttaphrynus melanostictus (Asian common toad)	1	**Fungi**	
Insects		*Ceratocystis fimbriata* (Ceratocystis blight)	1
Icerya purchasi (cottony cushion scale)	11	*Cryphonectria parasitica* (blight of chestnut)	1
Bactrocera cucurbitae (melon fly)	9	*Pseudocercospora fijiensis* (black Sigatoka)	1
Bactrocera dorsalis (Oriental fruit fly)	9	**Oomycetes**	
Arachnids			
Mononychellus tanajoa (cassava green mite)	1	**Bacteria and protozoans**	
Rhipicephalus microplus (cattle tick)	1	*Vibrio cholerae* (cholera)	9
		Yersinia pestis (black death)	1

2.4.2.3. Microorganisms

In general, microbial biological invasions are more readily detected in well-surveyed regions, such as Europe, than in less well-surveyed regions, such as Africa, highlighting the importance of monitoring programmes at continental and inter-continental scale (Waage et al., 2008). Fungi, oomycetes, and other microorganisms are poorly studied in most areas of the African continent. While Africa has been a source for several plant, animal, and human diseases (Bryant et al., 2007; Costard et al., 2009; Pretorius et al., 2010), reports of biological invasions across most of Africa have declined over the years, except for South Africa (Zengeya et al., 2020), most likely due to a lack of resources dedicated to this research. Thus, reliable data are scarce and mostly limited to a few well-researched regions, such as the Cape region (Crous et al., 2006) where the introduction and impact of alien fungal species are best documented (Wood, 2017). In South Africa, nine alien pathogenic species are known to attack native plants, while 23 host-specific pathogens of alien plant species have likely been introduced together with their hosts (Wood, 2017). In addition, one fish pathogen, 11 alien saprotrophic species, and 61 species of alien fungi forming ectomycorrhizae have been reported (Wood, 2017). Furthermore, seven host-specific alien pathogens have been introduced for the biological control of invasive alien species (Wood, 2017).

Compared to other IPBES regions, Africa has the lowest number of known alien macrofungi, with 107 species (Monteiro et al., 2020). Of these, 40 per cent belong to Agaricales, 29 per cent to Boletales and 13 per cent to Russulales. The most widespread macrofungi are *Pyrrhoderma noxium*, *Amanita muscaria* (fly agaric), *Pisolithus albus* (white dye-ball fungus), *Rhizopogon luteolus* (yellow false truffle), and *Suillus granulatu*s (weeping bolete mushroom), having been recorded for 8 or more countries. The highest numbers of alien macrofungi are reported for South Africa (65), Tanzania (25), Morocco (10), and Kenya (10). A number of countries, mainly from the Central African region, have between 1 to 5 known alien species.

2.4.2.4. Islands

Invasive alien species on islands are a major concern in the western Indian Ocean islands, including Comoros, Mauritius, Seychelles, Île de la Réunion, and smaller nearby islands where mammal predators such as cats and rats and plants negatively affect the increasingly disturbed ecosystems (Bonnaud et al., 2011; Kueffer et al., 2004; Russell et al., 2016; Russell & Le Corre, 2009; Tassin & Laizé, 2015). Île de la Réunion is estimated to have over 2,000 alien plant species, with more than 100 of these classified as invasive (e.g., *Leucaena leucocephala* (leucaena), *Hiptage benghalensis* (hiptage), *Ulex europaeus* (gorse) (Baret et al., 2006; Soubeyran et al., 2015). Of the

28 island groups, including 68 archipelagos present in the Western Indian Ocean, alien mammals can be found on each group with an average richness of five species per island group (Russell et al., 2016). There are 12 invasive alien mammal species on Île de la Réunion and various combinations of six of them on the nearby Îles Éparses (Russell & Le Corre, 2009). The islands of East Africa are major hubs of alien reptiles and amphibians globally: Mauritius and Île de la Réunion are inhabited by 17 and 15 alien species, respectively (Capinha et al., 2017; Kraus, 2009; Telford et al., 2019). On Socotra, 88 alien plants have been recorded (Senan et al., 2012). The recent invasion of Madagascar by *Duttaphrynus melanostictus* (Asian common toad) and some alien marine biota poses a severe threat to the native biodiversity of this island (Licata et al., 2019; B. M. Marshall et al., 2018). Similarly, the islands off the Western coast of Africa have repeatedly experienced animal invasions. In São Tomé and Principe, invasions began in the 1470s and by the end of the twentieth century, 14 alien mammal species were established on São Tomé and 12 on Principe (Dutton, 1994). Currently, 25 alien and invasive alien animal species are reported for both islands, of that 5 are birds, 2 ray-finned fish, 13 mammals, 4 insects, and 1 gastropod (De Menezes & Pagad, 2020). In Cabo Verde harbour there are 448 introduced plant taxa, equivalent to 60 per cent of the native flora, according to the Cabo Verde Biodiversity Database (Medina et al., 2015). In addition, there are 38 alien and invasive alien animal species, including 4 ray-finned fishes, 2 gastropods and 2 marine invertebrates, 4 reptile species, 6 bird species, 10 mammal species, and 9 insect species (Martinez et al., 2021).

2.4.2.5. Data and knowledge gaps

Although impacts of invasive alien species on Africa's biodiversity and ecosystem services are well known, there are still large gaps in scientific information (Egoh et al., 2020; Faulkner et al., 2015). With the exception of South Africa (B. W. van Wilgen et al., 2020), these gaps are apparent in many subregions, particularly in East Africa and adjacent islands, both for units of analysis and many taxonomic groups. The number of documented alien species in many countries may be significantly underestimated as this is a function of information availability, research intensity, and country development status (McGeoch et al., 2010).

For alien mammals, gaps exist for most of the African continent except for areas such as the western Mediterranean coast, South Africa, Madagascar, and adjacent islands. Knowledge of alien amphibians and reptiles is incomplete due to a lack of data (Capinha et al., 2017; García-Díaz et al., 2015; Kraus, 2009; Seebens, Blackburn, et al., 2017; N. J. van Wilgen et al., 2018). These gaps broadly match the distribution of data-deficient native reptile and amphibian species, which suggests a general scarcity of information about the status of reptiles and amphibians in the region (Böhm et al., 2013; Stuart et al., 2008). Further survey efforts in these data-poor areas can be expected to uncover established populations of alien amphibians and reptiles.

One of the main data gaps regarding freshwater invasions in Africa relates to the understanding of their geographical scope, given that most comprehensive reviews have been produced for South Africa only. A large taxonomic bias was also found, with reviews on faunal invasions, particularly fish invasions, or on specific species such as the highly invasive *Pontederia crassipes* (water hyacinth), dominating the literature, and many fewer studies on other taxonomic groups (Coetzee et al., 2019). Thus, the status of alien and invasive alien species presented here certainly underestimates the true number of freshwater invasive alien species present in the region. Increased research could help to better inform the trends and status of freshwater invasive alien species in Africa.

For vascular plants, Africa is geographically covered completely by the GloNAF database (Pyšek, Pergl, et al., 2017; van Kleunen et al., 2015, 2019), providing data on alien plant species in individual countries, but of varying quality (Pyšek, Pergl, et al., 2017) so that information remains scarce in some regions.

Information on the occurrence of alien fungi is missing for many African countries, mainly in North Africa, East Africa, and adjacent islands. The most complete information is available for South Africa, but even here knowledge is considered incomplete (Wood, 2017). The low number of alien macrofungi reported in most countries is likely a consequence of low research intensity and numbers are certainly underestimated.

2.4.3. Trends and status of alien and invasive alien species in the Americas

This section reports on the trends and status of alien species of the Americas (**Figure 2.31**, **Table 2.21**) for animals (**section 2.4.3.1**), plants (**section 2.4.3.2**), microorganisms (**section 2.4.3.3**), and islands (**section 2.4.3.4**), and provides an overview of data and knowledge gaps (**section 2.4.3.5**). A description of IPBES regions and sub-regions including a spatial representation is provided online (IPBES Technical Support Unit On Knowledge And Data, 2021) and in **Chapter 1**, **section 1.6.4**.

2.4.3.1. Animals

Trends

The number of alien animals in the Americas has increased across all taxonomic groups, especially post-1850, and across all subregions (**Figure 2.31**). Particularly steep increases are observed for North America, followed by South America, with the exception of alien birds which also showed steep increases in the Caribbean. Since 1900 the rates of increase have remained stable (e.g., mammals), declining (fishes in North America), or distinctly increasing (arthropods). Increases in numbers of alien arthropods in North America have been shown in several studies (Aukema et al., 2010; Mattson et al., 1994; Nealis et al., 2016) as well as in South America (Fuentes et al., 2020), for freshwater (Ricciardi, 2001, 2006) and for marine animals (Carlton & Eldredge, 2009; Cohen & Carlton, 1998; Ruiz, Fofonoff, et al., 2000). Transfers of species within a continent contribute to the spread and new incidences of alien species occurrences. Within the United States, for example, over 580 freshwater species have been introduced from one watershed to another outside their historical ranges; these introductions are nearly as numerous as those originating from outside the country, and they have increased over time, more than doubling in number since 1950 (USGS, 2021).

Alien mammal introductions in the Americas date to pre-Columbian times in the Caribbean islands for hunting (e.g., *Didelphis marsupialis* (common opossum), *Dasyprocta leporina* (agouti), *Dasypus novemcinctus* (nine-banded armadillo)) (Biancolini et al., 2021; Giovas et al., 2012; Long, 2003). European colonialism caused a surge in introductions of alien species beginning in the fifteenth century and peaking during the twentieth century, with a strong focus on game species and, more recently, on pets (Biancolini et al., 2021; Long, 2003).Considered collectively, the number of alien amphibians and reptiles in the Americas has been increasing since the 1950s and the introduction of new alien species through the pet trade is predicted to either accelerate or remain steady (Kraus, 2009; Lockwood et al., 2019; Perella & Behm, 2020; Powell et al., 2011; Seebens, Blackburn, et al., 2017; Stringham & Lockwood, 2018).

The first introductions of alien aquatic species in South America occurred in the 1500s in conjunction with European colonization, but remained relatively low until the1800s and 1900s, when they moderately increased. Alien aquatic introductions began increasing distinctly in the mid 1900s, both in South and North America, as shown in **Figure 3.6** in the IPBES Regional Assessment Report on Biodiversity and Ecosystem Services for the Americas (IPBES, 2018b). Through the 2000s there has been a large increase in the number of records and studies of alien organisms (e.g., Frehse et al., 2016; Vitule et al., 2021). Current data trends show no signs of slowing, either in terms of the number of alien species or in new spatiotemporal records (e.g., Vitule et al., 2021). Aquaculture and the aquarium trade (including e-commerce) are the most important pathways for the introduction of new alien species (e.g., Bezerra et al., 2019; Magalhães

et al., 2020; Vitule et al., 2019). Habitat alteration, the elimination of biogeographic barriers (e.g., D. A. dos Santos et al., 2019; Vitule et al., 2012), ballast water, hull fouling (Frehse et al., 2016), and introducing fish for angling are other important mechanisms for introduction that have direct effects on both biodiversity and socio-economic aspects (e.g., Doria et al., 2020; Vitule et al., 2014).

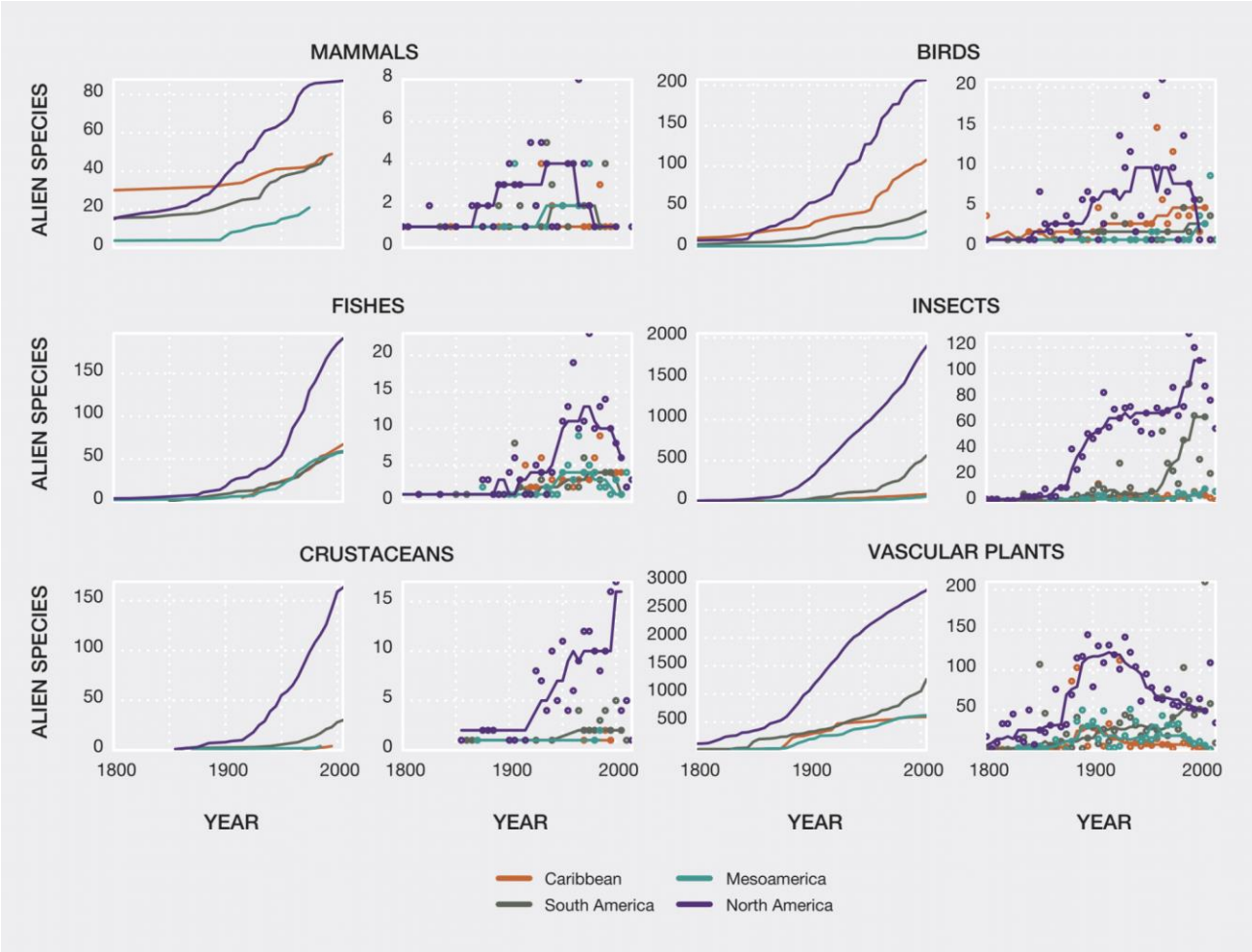

Figure 2.31. Trends in numbers of established alien species for the Americas. The cumulative numbers (left panels) and number of established alien species per five-year intervals (right panels). Numbers shown here underestimate the real extent of alien species occurrences due to a lack of data. Lines in right panels indicate smoothed trends calculated as running medians (**section 2.1.4** for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

For marine alien species in American waters, seminal studies have highlighted the rising numbers of marine alien species (Cohen & Carlton, 1998; Coles et al., 1999). Recent updates for regions such as for the coastal waters of the American temperate zones found an increase in the total number of detected alien species, while the rate of newly recorded alien species has remained stable in recent decades (Bailey et al., 2020). Teixeira & Creed (2020) reported that the number of introduced species increased by 160 per cent for Brazil between 2009 and 2019. A rise in the number of detected alien species was also found for Argentina and Uruguay (Schwindt et al., 2020), where the number of detections increased by a factor of 4.5 between 2001 and 2019, with an estimated arrival of one new species every 178 days.

Status

The Americas host a significant number of established alien mammals (96 species) from nine orders and 29 families. Most are from the orders Cetartiodactyla (30 species), Rodentia (28 species), Primates (14 species) and Carnivora (11 species) (Biancolini et al., 2021). Within the Americas, alien mammal richness is high on the east coast of North America, Alaskan islands, Newfoundland Island, central-southern United States, the Caribbean Archipelago, and Patagonia (Malvinas) (Biancolini et al., 2021). Many mammals native to the Americas have been translocated inside the region and are thus classified as being alien (53 species), while the major outside donors were Europe and Central Asia (8 species), followed by Asia and the Pacific (7 species) and Africa (2 species). Alien mammal introductions mainly occurred for sport hunting, the pet trade, so called "faunal improvement" (e.g., releases carried out to aesthetically modify the landscape), farming, and zoos (Biancolini et al., 2021). A well-established hunting industry in North America fuels the introduction of ungulates, frequently contained in large enclosures in the southern United States and Mexico or directly released into the wild (Long, 2003). For example, *Ammotragus lervia* (aoudad), a bovid native to the Northern African savanna and desert areas, is now established in a large range north of Mexico (establishment not reported for Mexico) (Texas Invasive Species Institute, 2021). One of the most invasive alien mammals in the Americas is *Herpestes javanicus auropunctatus* (small Indian mongoose) established on many islands in the Caribbean (Biancolini et al., 2021; Hays & Conant, 2007; Louppe et al., 2020). This species was widely introduced during the nineteenth century as a biological control agent for rodents, and it is considered one of the "100 worst invasive alien species in the world" because of its generalist diet and high predatory efficiency. Another high-profile example of mammal invasion is the ongoing spread of *Hippopotamus amphibius* (so-called "Escobar's hippos"; hippopotamus) in the Magdalena River of Colombia (Biancolini et al., 2021; Jarić et al., 2020). Four individuals of this large African mammal were introduced by Pablo Escobar in the 1980s for his amusement and they escaped captivity in 1993 after his death (Dembitzer, 2017); in 2020, about 80–120 alien hippos were found to occur over 2000 km^2.

Alien bird species are particularly rich in North America, notably Florida and California, where several alien parrot species have established populations (E. E. Dyer, Cassey, et al., 2017). Alien parrots are also widespread in South America. Attempts to establish all the bird species mentioned in Shakespeare's works into North America have a legacy in the distribution of *Sturnus vulgaris* (common starling) across the continents.

In South America, the number of reported alien aquatic organisms (ranging from microscopic fungi, invertebrates, and plants to large mammals (Schwindt et al., 2018) is increasing rapidly (e.g., Fuentes et al., 2020; Vitule et al., 2021), with fish and molluscs (26.8 per cent and 25.2 per cent of studied invasive alien marine species respectively; see Schwindt & Bortolus, 2017, **Figure 2.31**) having the largest number of studies, species, and spatiotemporal occurrence records (e.g., (Bezerra et al., 2019; Frehse et al., 2016; Vitule et al., 2021). The most recent records of fishes in South America indicate that over 75 alien species have been translocated between different basins within South America (Bezerra et al., 2019; Vitule et al., 2019) and more than 80 alien fish species have been introduced from other regions of the world (Doria et al., 2021; Vitule et al., 2019, 2021). Most of the alien aquatic species studied in South America belong to the salmonid and cichlid families, but *Limnoperna fortunei* (golden mussel) is the alien species included in the most publications within the region (Schwindt & Bortolus, 2017).

Table 2.22. Numbers of established alien species for subregions of the Americas

Numbers of alien species can vary depending on data sources. For mammals, birds and vascular plants, ranges of values indicate variation among databases (**section 2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the

text due to variation among data sources. A data management report for the data underlying this table is available at https://doi.org/10.5281/zenodo.7615582

	Caribbean	Mesoamerica	North America	South America	Total
Mammals	35-62	8-34	49-95	25-77	83-164
Birds	110-113	29-41	210-211	53-114	249-287
Fishes	91	226	619	144	803
Reptiles	60	60	121	56	192
Amphibians	20	8	41	16	62
Insects	153	163	2,116	640	2,636
Arachnids	33	36	168	76	207
Molluscs	26	60	212	68	255
Crustaceans	10	64	173	79	248
Vascular plants	1,402-1,761	1,600-2,242	6,571-7,424	2,492-3,099	8,005-9,325
Algae	4	105	65	50	193
Bryophytes	0	0	34	21	48
Fungi	17	15	174	219	363
Oomycetes	2	2	7	5	12
Bacteria and protozoans	1	4	6	5	14
Total	2,036-2,425	2,612-3,292	11,587-12,487	4,353-5,073	13,370-14,809

North America has a long and very well-studied history of aquatic species introductions, particularly for fish (e.g., Courtenay & Meffe, 1989; Fuller et al., 1999; Moyle, 1986). Introductions of European and Asian species that have also been introduced worldwide are noteworthy, such as *Salmo trutta* (brown trout) or *Cyprinus carpio* (common carp), species of tropical or subtropical origin introduced to Florida, and species from elsewhere in the United States introduced to California, and more recently *Cyprinus carpio* in the Mississippi Basin. The Laurentian Great Lakes have many invasive alien animals of Ponto-Caspian origin (**Box 2.9**), mostly introduced through ballast water (Ricciardi & MacIsaac, 2000; Vanderploeg et al., 2002). *Pterois* species (lionfishes) have spread through the western Atlantic, including parts of North America and the Caribbean. The introduction of *Oreochromis niloticus* (Nile tilapia), *Salmo trutta*, *Cyprinus carpio*, and many other fish species is widespread throughout the Americas (e.g., Agostinho et al., 2005; Contreras-Balderas et al., 2008; Habit et al., 2010, 2015). Similarly, many species native to small parts of the American continent (e.g., *Gambusia* spp. (Gambusias), *Oncorhynchus mykiss* (rainbow trout), *Poecilia reticulata* (guppy)) have been widely introduced throughout the Americas and elsewhere (Marr et al., 2013).

The Americas is the IPBES region with the highest number of alien reptiles and amphibians (**Table 2.22**). Within this region, the United States is home to several hotspots of alien amphibians and reptiles (Capinha et al., 2017; Kraus, 2009; Krysko et al., 2011, 2016). Florida (58 species established), California (25 species), and Puerto Rico (11 species) stand out as global hotspots of alien amphibians and reptiles (Capinha et al., 2017; Kraus, 2009; Krysko et al., 2011, 2016; Meshaka, 2011; Perella & Behm, 2020; Powell et al., 2011). Besides Puerto Rico, other Caribbean islands such as Cuba and the Bahamas are also important global hotspots (Borroto-Páez et al., 2015; Capinha et al., 2017; C. R. Knapp et al., 2011; Kraus, 2009; Powell et al., 2011). In South America, Brazil is the country with the highest number of alien amphibians and reptiles, with a total of 136 species recorded, of which at least seven have established wild populations (Capinha et al., 2017; É. Fonseca et al., 2019; Kraus, 2009).

Marine alien species across the Americas are unequally studied geographically and taxonomically, and compilations are scarce over time and space. Comprehensive assessments are lacking even in well-studied regions, such as the United States, making it difficult to draw general conclusions (Bailey et al., 2020). The first comprehensive assessment was made for the United States for continental coasts finding 298 marine alien species (Ruiz, Fofonoff, et al., 2000). However, this assessment needs updating, that is, as of 2006 there are 257 introduced species in California alone (Ruiz et al., 2011). The reports in the rest of North America and mesoamerica are spatially or taxonomically focused and no comprehensive compilations have been published. The Southwestern Atlantic is the best-known region in South America for marine invasive alien species, yet, unequally studied among countries and sub-regions (Schwindt & Bortolus, 2017). Brazil has the highest number of marine alien species with 138 species (Teixeira & Creed, 2020), followed by Argentina and Uruguay with 129 species (Schwindt et al., 2020). On the Pacific coast, Chile reported 51 alien species (Castilla & Neill, 2009; Villaseñor-Parada et al., 2017), and Colombia 4 (Gracia et al., 2011), but this may be due to lack of research (Schwindt & Bortolus, 2017).

2.4.3.2. Plants

Trends

Over the last two centuries the cumulative rate of increase in established alien plant species was most rapid in North America, quickly accelerating at the end of the nineteenth century (**Figure 2.31**; Lavoie et al., 2012; Pyšek et al., 2019). South America exhibited a slower cumulative increase, likely due to fewer experts and lower research intensity when compared to North America (Frehse et al., 2016; Schwindt et al., 2020; Schwindt & Bortolus, 2017).(Fuentes et al., 2008; Rojas-Sandoval & Acevedo-Rodríguez, 2015; Ugarte et al., 2010). Numbers of alien plant species are expected to increase over the next 20 years in emerging South American economies such as Brazil, Mexico, and Argentina based on global trade dynamics and climate change (Seebens et al., 2015) which could reverse the current status of North America as more invaded by plants than South America (Pyšek et al., 2019).

Status

With 5,958 established alien vascular plant species, North America has the highest recorded alien plant richness in the world (Pyšek, Pergl, et al., 2017; van Kleunen et al., 2015). South America harbours 2,667 established alien plants (Pyšek et al., 2019); note that the numbers differ from those presented in **Table 2.21**, because of different data sources and deviating data integration steps (**section 2.1.4** for further details). In the United States, California is the world's richest region in terms of established alien vascular plants with 1,753 established alien plant species, and Florida is a world regional hotspot with 1,473 established alien plants (Kartesz, 2014). *Sonchus oleraceus* (common sowthistle), *Plantago major* (broad-leaved plantain), *Taraxacum officinale* (dandelion), and *Poa annua* (annual meadowgrass) are among the most widely distributed established species in North America (each in more than 85 regions), while for South America the analogous list includes *Eleusine indica* (goose grass), *Sonchus oleraceus*, *Plantago major*, *Polygonum aviculare* (prostrate knotweed), and *Brassica rapa* (field mustard) (Pyšek, Pergl, et al., 2017; **Table 2.23**). According to Pyšek, Pergl, et al. (2017), countries in Mesoamerica also harbour many established alien plants (Nicaragua 671, Mexico 519, Costa Rica 280, Panama 263), but due to their high native diversity, alien plants make up only 2.0–2.8 per cent of the total floras, the exception being Nicaragua with 10.4 per cent (e.g., Correa A. et al., 2004; Pyšek, Pergl, et al., 2017; Chacón & Saborío, 2012). Some regions in the Caribbean are heavily invaded by established alien plants, both in terms of actual species numbers (Cuba 542, Bahamas 356) or the proportion of established alien plants in the national floras (Bahamas 24 per cent, Barbados 14 per cent). Other countries in the Caribbean harbour 20 to 110 established alien plant species and their contributions to national floras do not exceed 8 per cent (Acevedo-Rodríguez & Strong, 2008; Kartesz, 2014; Pyšek, Pergl, et al., 2017).

Table 2.23. Top most widespread invasive alien species for the Americas

The number of regions where the species has been recorded and classified as being invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distributions of invasive alien species rather than their impacts which are covered in **Chapter 4**. A maximum of three species is shown for each group (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species name	**No. of regions**	**Species name**	**No. of regions**
Mammals		**Molluscs**	
Rattus rattus (black rat)	21	*Lissachatina fulica* (giant African land snail)	12
Mus musculus (house mouse)	19	*Melanoides tuberculata* (red-rimmed melania)	9
Rattus norvegicus (brown rat)	19	*Corbicula fluminea* (Asian clam)	8
Birds		**Crustaceans**	
Passer domesticus (house sparrow)	11	*Macrobrachium rosenbergii* (giant freshwater prawn)	6
Columba livia (pigeons)	10	*Cherax quadricarinatus* (redclaw crayfish)	5
Bubulcus ibis (cattle egret)	5	*Carcinus maenas* (European shore crab)	2
Fishes		**Vascular plants**	
Cyprinus carpio (common carp)	9	*Calotropis procera* (apple of sodom)	13
Oreochromis niloticus (Nile tilapia)	9	*Leucaena leucocephala* (leucaena)	13
Oncorhynchus mykiss (rainbow trout)	8	*Ricinus communis* (castor bean)	13
Reptiles		**Algae**	
Hemidactylus mabouia (tropical house gecko)	7	*Undaria pinnatifida* (Asian kelp)	4
Hemidactylus frenatus (common house gecko)	6	*Codium fragile* (dead man's fingers)	2
Anolis sagrei (brown anole)	4	*Didymosphenia geminata* (didymo)	2
Amphibians		**Bryophytes**	
Lithobates catesbeianus (American bullfrog)	11	*Campylopus introflexus* (heath star moss)	1
Rhinella marina (cane toad)	6	**Fungi**	
Xenopus laevis (African clawed frog)	4	*Batrachochytrium dendrobatidis* (chytrid fungus)	6
Insects		*Amanita phalloides* (death cap)	1

Icerya purchasi (cottony cushion scale)	11	*Bipolaris maydis* (southern corn leaf blight)	1
Maconellicoccus hirsutus (pink hibiscus mealybug)	11	**Oomycetes**	
Aedes albopictus (Asian tiger mosquito)	10	*Phytophthora cinnamomi* (Phytophthora dieback)	1
Arachnids		*Phytophthora lateralis* (Port-Orford-cedar root disease)	1
Raoiella indica (red palm mite)	7	*Phytophthora ramorum* (sudden oak death)	1
Aceria litchii (Litchi gall mite)	1	**Bacteria and protozoans**	
Avicularia avicularia (tarantula spiders)	1	*Vibrio cholerae* (cholera)	5
		Yersinia pestis (black death)	2

2.4.3.3. Microorganisms

Trends

The introduction of microorganisms has a long history in the Americas but is poorly documented as is the case worldwide. Where available, studies on the trends in alien microorganisms usually cover only fungi. For example, first records of alien fungi in Chile have been documented from the early twentieth century and show a continuous increase in numbers until the present (Fuentes et al., 2020).

Status

The Americas harbour at least 199 alien macrofungi species, with approximately 36 per cent belonging to the group Agaricales, 32 per cent to Boletales and 11 per cent to Russulales (Monteiro et al., 2020). Species most widely distributed within the region are *Suillus luteus* (ectomycorrhizal fungus of pine), *Amanita muscaria* (fly agaric), *Rhizopogon roseolus* (ectomycorrhizal fungus), and *Suillus granulatus* (weeping bolete mushroom). Countries with high numbers of known established species occur mainly in South America, and include Brazil (75), Argentina (60), and Chile (40) (Monteiro et al., 2020). In the remaining IPBES sub-regions, higher numbers of known alien macrofungi were found in the United States (including Hawaii) (50), Canada, and Mexico (7 each).

2.4.3.4. Islands

Alien and invasive alien species are widespread on islands of both sides of the Americas: in the Pacific Ocean (notably the Galapagos islands) and the Atlantic Ocean (notably the Caribbean islands; e.g., (Kairo et al., 2003; Rojas-Sandoval & Acevedo-Rodríguez, 2015; Van der Burg et al., 2012). As an example, Caribbean Island forests are extensively dominated by alien tree species (Brandeis et al., 2009; Chinea & Helmer, 2003; Helmer et al., 2012), some of which are shade-tolerant and could permanently change forest species composition (C. J. Brown et al., 2006). In addition, several alien species grow in forest plantations, livestock pastures, and abandoned agricultural fields creating both economic and environmental impacts. Such is the case for *Dichrostachys cinerea* (sickle bush), an alien species that occurs across almost 800,000 hectares in Cuba (Hernández et al., 2002). The Hawaiian Islands are a global hotspot of plant invasions with 1,488 total alien plant species, and numbers for individual islands within the archipelago ranging from 386 to 913 alien species (Imada, 2012).

On the other side of the Americas, the Galapagos Archipelago harbours an estimated 1700 alien species with *Capra* sp. (goat) and *Rubus niveus* (Mysore raspberry) being among the most common until recently (Toral-Granda et al., 2017). Between the 1980s and 1990s, the number of introduced plants has nearly doubled on the Galapagos Islands, reaching nearly 900 species (De Lourdes Torres & Mena, 2018). In addition, a study of the residence time and human-mediated propagule pressure of plants suggested that this archipelago is still in an early stage of plant invasions, due to the booming tourism industry and increasing human population size (Trueman et al., 2010).

2.4.3.5. Data and knowledge gaps

Data availability for the Americas is dominated by studies from North America. Across taxonomic groups, the Caribbean, Mesoamerica, and South America have considerably less data available relative to North America (Pyšek et al., 2008). Studies on the temporal accumulation of alien species are almost exclusively available for this region except for a few studies for islands in the Caribbean and South America (Fuentes et al., 2008; Rojas-Sandoval & Acevedo-Rodríguez, 2015; Toral-Granda et al., 2017). Only a few studies on temporal trends exist for mainland South America or Mesoamerica (e.g., Fuentes et al., 2020). Temporal information is scarce for most taxonomic groups in North America, including well-investigated groups such as vascular plants, birds, and mammals. For some groups, that are generally less studied globally, such as many invertebrates, fungi, and microorganisms, information is lacking for vast areas of this region.

In South America, regions often considered pristine and less impacted, such as the Amazon basin, lack studies on alien species and could be more thoroughly explored, particularly given recent levels of deforestation which could facilitate biological invasions (e.g., Frehse et al., 2016; Vitule et al., 2021; **Chapter 3, section 3.3.1**). In addition, there is a high degree of uncertainty on the status of alien species or populations and due to uncertainties about the native range of many species, the challenge of cryptic invasive alien species may be even greater for South America than the rest of the world (Bortolus et al., 2015; Essl et al., 2018; Jarić et al., 2019).

A notable exception represents alien amphibians and reptiles which are relatively well-known in most of the Americas as a consequence of ongoing surveys and research (Capinha et al., 2017; É. Fonseca et al., 2019; García-Díaz et al., 2015; González-Sánchez et al., 2021; Kraus, 2009; Krysko et al., 2016; Perella & Behm, 2020; N. J. van Wilgen et al., 2018). Nevertheless, clarification of the status (i.e., being alien or native to a certain region) of some species in Mesoamerica and South America is needed (García-Díaz et al., 2015; González-Sánchez et al., 2021), and further work will improve the understanding of the ecology and impacts of the alien amphibians and reptiles present in this region (É. Fonseca et al., 2019; N. J. van Wilgen et al., 2018).

An important data gap exists for countries along the North Atlantic coast of South America (from French Guiana to Guiana; Schwindt & Bortolus, 2017). For example, in Venezuela the number of marine alien species originally reported by Pérez et al. (2007) was 22 but was later lowered to 11 alien species by Figueroa López and Brante (2020) due to uncertainty in the provided records. However, the number of marine alien species is likely higher even than the number reported by Pérez et al. (2007). No extensive compilations of alien species in general are available for continental Ecuador and for Peru (but see Calder et al., 2021; Cárdenas-Calle et al., 2019).

The availability of records on alien macrofungi for the Americas is dominated by a few countries, notably those for which higher numbers of alien species are reported here, including Argentina, Brazil, Chile and the United States. Important data gaps on established alien species exist for many other countries of the Americas, particularly in the Caribbean and Mesoamerica (Monteiro et al., 2020). In general, information about alien microorganisms is lacking for all of the Americas as is the case for other IPBES regions.

2.4.4. Trends and status of alien and invasive alien species in Asia and the Pacific

This section reports on the trends and status of alien species of Asia and the Pacific for animals (**section 2.4.4.1**), plants (**section 2.4.4.2**), microorganisms (**section 2.4.4.3**), and islands (**section 2.4.4.4**), and provides an overview of data and knowledge gaps (**section 2.4.4.5**). A description of IPBES regions and sub-regions including a spatial representation is provided online (IPBES Technical Support Unit On Knowledge And Data, 2021) and in **Chapter 1**, **section 1.6.4**.

2.4.4.1. Animals

Trends

The numbers of alien animal species increased continuously for all taxonomic groups and all subregions of the Asia-Pacific regions (**Figure 2.32**). The steepest increases were observed in Oceania for all animal groups considered in **Figure 2.32**, except for fishes. In Oceania, the number of alien animals rose distinctly already in the nineteenth century, much earlier relative to other subregions where steep increases were mostly observed after 1950. Northeast Asia experienced strong increases during that time for birds, fishes, and crustaceans. Likewise, increasing alien species numbers have been reported in various countries for insects (Huang et al., 2011; Yamanaka et al., 2015), gastropods (Barker, 1999; Roll et al., 2009), amphibians and reptiles (Lee et al., 2019), and marine alien species of different groups (Bailey et al., 2020; Hewitt et al., 2004).

Before colonization by Europeans, alien mammals in South-East Asia were introduced via ancient exchanges between the Indonesian Archipelago, Papua New Guinea, and Australia with numerous prehistoric introductions of game, fur, pet, and stowaway species (e.g., *Phalanger orientalis* (northern common cuscus), *Sus celebensis* (Sulawesi pig), *Dendrolagus matschiei* (Matschie's tree-kangaroo)) (Biancolini et al., 2021; Heinsohn, 2003; Long, 2003). Introductions surged during the nineteenth century following European colonization when Australia, New Zealand, and other Pacific islands became hotspots for alien mammals that negatively impacted native animal communities (Biancolini et al., 2021; Woinarski et al., 2015). The aim was to supply game species (e.g., *Cervus elaphus* (red deer), *Lepus europaeus* (European hare), *Dama dama* (fallow deer)) or create a familiar environment for colonists. In Central Asia and North-East Asia, alien mammal introductions were largely carried out at the beginning of the nineteenth century to create hunting and furbearing populations (Biancolini et al., 2021; Clout & Russell, 2008; Long, 2003). Native Australian species became the subject of conservation introductions, also called assisted colonization, to offshore islands free of invasive alien mammals (Seddon et al., 2015; Woinarski et al., 2015).

The Asia-Pacific region has experienced a growing number of alien bird, reptile and amphibian introductions, a trend likely to continue in the future (Chapple et al., 2016; Kraus, 2009; Lee et al., 2019; Pili et al., 2020; Seebens, Bacher, et al., 2021; Seebens, Blackburn, et al., 2017; Toomes et al., 2020).

The number of alien freshwater species grew slowly in Asia and the Pacific until the nineteenth century (**Figure 2.32**) when the number of recorded alien freshwater species distinctly increased (H. H. Tan et al., 2020; Yuma et al., 1998). During the twentieth century, aquaculture was the main pathway for freshwater fish species introductions (Saba et al., 2020; Xiong et al., 2015) and in the beginning of the late twentieth century, many freshwater fish species were introduced for ornamental purposes (H. H. Tan et al., 2020; Yuma et al., 1998). The number of ornamental freshwater fish rapidly increased towards the end of the twentieth century and ornamental trade is now the main pathway of introduction (Goren & Ortal, 1999; Saba et al., 2020; Yuma et al., 1998).

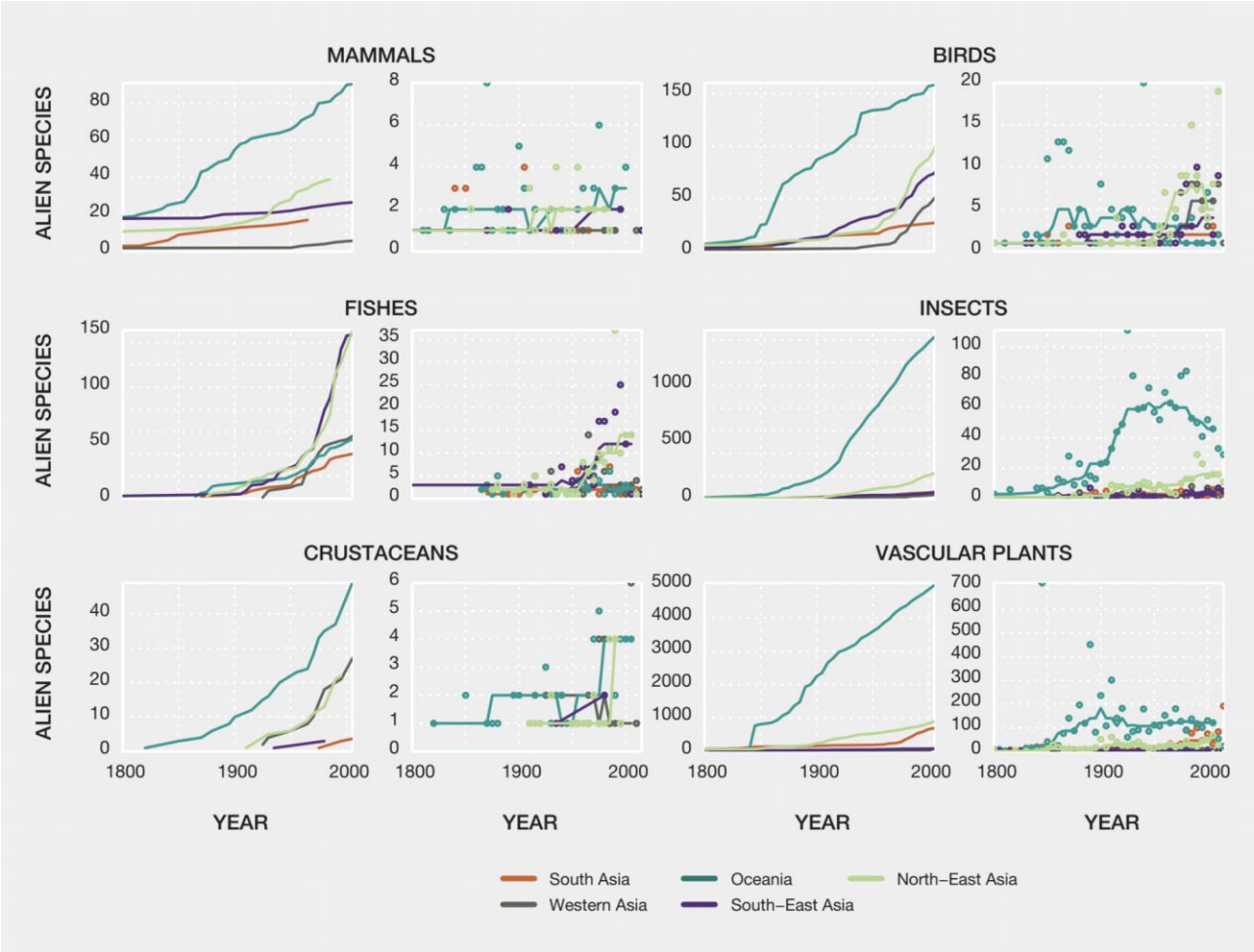

Figure 2.32. Trends in numbers of established alien species for Asia and the Pacific. Cumulative numbers (left panels) and number of established alien species per five-year intervals (right panels). Numbers shown here underestimate the actual extent of alien species occurrences due to a lack of data. Lines in right panels indicate smoothed trends calculated as running medians (**section 2.1.4** for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

As in many other regions, detected numbers of introduced alien marine species in the South Pacific region increased over time. The first assessment for New Zealand documented 129 alien species (Cranfield et al., 1998), while the most recent assessment nearly doubled that number to 214 (Therriault et al., 2021), with 15 alien species considered as new arrivals establishing between 2010 and 2018. Despite these numbers, recent work shows an apparent decline in primary detections since 2005 in several regions across Asia and the Pacific. It is unknown if this decline is a result of effective preventive strategies (**Chapter 5**, **section 5.5.1**) or a reduction in search effort (Bailey et al., 2020). In Asia, alien species introductions occur mainly by unintentional translocations such as ballast water discharged in ports located across China's coast (Y. Chen et al., 2017).

Status

Asia and the Pacific is the region with the highest number of established alien mammals in the world (130 species), from 12 orders and 34 families (Biancolini et al., 2021). The majority are from the orders Cetartiodactyla (30), Diprotodontia (28), Rodentia (26) and Carnivora (21). Areas with high numbers of alien mammals are Japan, the Indonesian archipelago, Australia, New Zealand, and the Pacific islands. These alien species originate mainly from within the region itself (96), while 14

alien species originate from Europe and Central Asia, 13 from the Americas, and 10 from Africa. Major pathways of alien mammal introductions in Asia and the Pacific are hunting (48 alien species), conservation (28), pet trade (27), faunal improvement (27), farming (22), stowaway transportation (16), and biocontrol (12) (Biancolini et al., 2021). During the nineteenth century acclimatization societies sought to "improve" local fauna by introducing many aesthetically pleasing and/or game species to Australia and New Zealand (Biancolini et al., 2021; Simberloff & Rejmanek, 2011). Of the 130 established alien mammal species, 68 (52 per cent) have invasive alien populations (Biancolini et al., 2021). Examples include the prolific generalist *Oryctolagus cuniculus* (rabbits), a well known invasive alien species in Australia (Kirkpatric et al., 2008), and the generalist *Trichosurus vulpecula* (brushtail possum), which was introduced to New Zealand in 1858 for domestic fur and meat trade (Forsyth et al., 2018; Gormley et al., 2012).

Table 2.24. Numbers of established alien species for subregions of Asia and the Pacific

Numbers of established alien species can vary depending on data sources. For mammals, birds, and vascular plants ranges of values indicate variation among databases (see **section 2.1.4** for further details on data sources and data processing). Note numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this table is available at https://doi.org/10.5281/zenodo.7615582

	North-East Asia	Oceania	South Asia	South-East Asia	Western Asia	Total
Mammals	28-53	50-105	12-28	38-54	5-20	97-163
Birds	119-129	169-175	29-38	84-85	84-139	287-336
Fishes	287	95	90	296	125	633
Reptiles	41	41	7	35	13	103
Amphibians	24	13	4	12	1	43
Insects	607	1,521	111	89	101	2,017
Arachnids	67	83	13	18	6	129
Molluscs	81	119	15	24	89	261
Crustaceans	43	75	12	19	63	158
Vascular plants	2,219-2,454	4,631-6,747	1,055-3,142	1,313-1,598	271-562	6,141-9,101
Algae	55	63	8	13	47	157
Bryophytes	0	32	0	0	0	32
Fungi	59	303	17	20	1	363
Oomycetes	9	5	2	1	0	12
Bacteria and protozoans	7	4	3	2	4	12
Total	4,008-4,278	7,963-10,140	1,490-3,602	2,053-2,355	932-1,293	10,445 - 13,520

Despite Asia and the Pacific having a larger area and more suitable habitats than Europe and Central Asia, the Asia-Pacific region harbours similar numbers of alien amphibians and reptiles as Europe and Central Asia (**Table 2.18**). This pattern may possibly be a result of stringent biosecurity measures (**Chapter 5**, **section 5.6.3.3**) in some areas such as Australia, New Zealand, and Japan, (Brenton-Rule et al., 2016; Chapple et al., 2016; García-Díaz et al., 2017; Toomes et al., 2020), but also lower relative research intensity in other regions (**Figure 2.6**). Despite the comparatively low alien species richness, the Asia-Pacific region harbours two of the best-known examples of alien

reptiles and amphibians, namely *Boiga irregularis* (brown tree snake) in Guam and *Rhinella marina* (cane toad) in Australia and other Pacific islands (Engeman et al., 2018; Lever, 2003; Rogers et al., 2017; Shine, 2018; Zug, 2013). The notable invasive alien species *Lithobates catesbeianus* (American bullfrog), *Trachemys scripta* (pond slider), and *Eleutherodactylus planirostris* (greenhouse frog) have been reported in China (S. Lin et al., 2017; X. Liu et al., 2015; Shi et al., 2009). Additionally, Japan (17 alien species), the Cook Islands (14 alien species), and island territories such as Taiwan, Province of China, (at least 12 alien species) and Guam, United States (11 alien species) are global hotspots of alien amphibians and reptiles (Capinha et al., 2017; Kraus, 2009; Lee et al., 2019; Zug, 2013).

In Asia, the number of introduced alien freshwater species is highest for China (439) (Xiong et al., 2015), followed by Malaysia (203 freshwater fishes) (Saba et al., 2020) and the Philippines (159 freshwater fishes) (Casal et al., 2007). The number of established alien freshwater fishes is highest in China (61) (Luo et al., 2019), followed by Singapore (42) (H. H. Tan et al., 2020), the Philippines (39) (Casal et al., 2007), and Japan (23) (Yuma et al., 1998). Most of the established alien fishes were introduced for aquaculture (Casal et al., 2007; Luo et al., 2019), while the proportion of introduced ornamental fishes is much lower (Casal et al., 2007; Luo et al., 2019).

A regional assessment of marine alien species across Asia and the Pacific is lacking, and, as in many other marine regions, records are likely underestimated. Lutaenko et al. (2013) compiled an atlas of marine invasive alien species in the Northwest Pacific Region, which includes territories from Japan, the Republic of Korea, the Russian Federation and China (Yellow Sea). For Japan, 42 marine alien species were reported (Iwasaki, 2006), mostly concentrated in eutrophicated enclosed bays near large urban cities such as Tokyo Bay and Osaka Bay. Although ballast water and hull fouling are important vectors, 21 species were reported as intentionally introduced for commercial sales, live bait, or fishery studies (Lutaenko et al., 2013). Partial updates were done by Doi et al. (2011) adding crustaceans (mainly crabs, amphipods, barnacles, and isopods) to the list of alien species reported by Iwasaki (2006), increasing the 42 by 10 reported alien species. There are few reports about marine species introductions to Korean and Chinese waters. Seo and Lee (2009) reported 136 species suspected to be alien across this vast region of Asia, while 41 alien species are recognized only for the Republic of Korea (Lutaenko et al., 2013). As for the Russian waters of the Northwest Pacific region, 37 marine invasive alien species were reported by 2010 and this number increased to 66 in a later assessment (Zvyagintsev et al., 2011), mostly concentrated around Peter the Great Bay in Russia. Two recent reports for the north Pacific document 73 alien species for the northern central Indo-Pacific, 208 species for the northwest Pacific (includes northeast Asia), and 368 for the northeast Pacific (from the United States, Canada up to Alaska; Kestrup et al., 2015; Lee II & Reusser, 2012). In conclusion, the vast region of the north Pacific has a similar number of introduced marine species as the Mediterranean Sea. In addition, the northwest Pacific contains the largest number of alien fishes (34 species), most intentionally released into the wild or maintained in aquaculture facilities.

There are few exhaustive assessments for the south Pacific Ocean with the greatest research efforts in Australia and New Zealand. Surveysof Port Phillip Bay (Australia) detected 100 marine alien species (Hewitt et al., 2004). A subsequent thorough literature reviewthat included data from port surveys yielded 132 alien species (Sliwa et al., 2008). As of March 2018 in New Zealand, 214 established alien species were reported (Therriault et al., 2018). The knowledge of marine bioinvasions of the Pacific Island Countries and Territories is scattered and dispersed in diverse publications. Surveys in Pago Pago Harbor (American Samoa) recognized 17 marine alien species (Coles et al., 2003), 40 alien species were detected from Guam (Paulay et al., 2002), and 11 alien species in Malakal harbour, Palau (M. L. Campbell et al., 2016). Most alien species were associated with transport in ballast water or biofouling (Hewitt & Campbell, 2010), and the number of intentional introductions for aquaculture purposes are low in Australia and New Zealand but high across the Pacific Islands countries (Eldredge, 1994). Many introduction attempts have been

conducted in the past 50 years in the south Pacific Ocean, with at least 38 alien species originating from small scale fisheries or aquaculture activities.

2.4.4.2. Plants

Trends

First records of alien plant species in Asia and the Pacific date back more than 1000 years (Wijesundara, 2010), and continual increases in the number of established alien species have been consistently recorded for several Asian and Pacific countries (Banerjee, 2020; C. Chen et al., 2017; Jaryan et al., 2013; Lazkov & Sultanova, 2011; Shrestha, 2016; Vinogradov & Kupriyanov, 2016; Wijesundara, 2010; Wu et al., 2010). The most dramatic increase in the cumulative number of alien plant species is recorded for Oceania, including Australia, New Zealand, and the Pacific Islands (**Figure 2.32**). Introduction rates peaked in around 1900, followed by a decline and a re-acceleration in the mid-twentieth century (**Figure 2.32**). The trends for other Asia-Pacific sub-regions are similar to that for Oceania but they have markedly lower absolute numbers of established alien species per time period.

Status

The Asia-Pacific region includes several global hotspots of established alien plant species (Dawson et al., 2017) as for islands in Oceania (Essl et al., 2019; Moser et al., 2018). Such hotspots include New Zealand with 1,726 established alien plant species (comprising 44.5 per cent of the flora; Howell & Sawyer, 2006), Tahiti with 1,346 (73.8 per cent), and Guam with 833 (66.5 per cent, Raulerson, 2006). Australian states harbour from 1,186 established alien species in Western Australia to 1,584 in New South Wales, corresponding to 12–25 per cent of the total plant diversity in these states (Pyšek, Pergl, et al., 2017; Randall, 2002; Walsh & Stajsic, 2007). Australasia experienced a rapid accumulation of established alien plants during colonization, while the Pacific islands show the steepest increase in established plant species among all global regions (van Kleunen et al., 2015). The most widespread established alien species on the Pacific Islands include *Euphorbia hirta* (garden spurge), *Cenchrus echinatus* (southern sandbur), *Phyllanthus amarus* (jamaicaweed), *Sida rhombifolia* (arrowleaf sida), *Carica papaya* (papaya), *Eleusine indica* (goose grass), and *Euphorbia prostrata* (prostrate sandmat). In Australia and New Zealand,the most widespread established alien species are *Sonchus oleraceus* (common sowthistle), *Solanum americanum* (American black nightshade), *Chenopodiastum murale* (nettle-leaf goosefoot), *Medicago polymorpha* (bur clover), and *Malva parviflora* (pink cheeseweed) (Pyšek, Pergl, et al., 2017; **Table 2.25**). Global hotspots of established alien species also occur in other Asian sub-regions; in South Asia and South-East Asia, India (471 alien plants comprise 2.6 per cent of the flora; Inderjit et al., 2018), the Philippines (628 species, 6.4 per cent; Pelser et al., 2011), and Indonesia (503 species, 1.7 per cent; Biotrop, 2003) are invasion hotspots. In Nepal, 21 established alien plant species have been classified as being invasive (Shrestha, 2016), while 101 invasive alien plant species have been recorded for Bhutan (Dorjee et al., 2020). In North-East Asia, Japan is richest in alien plants (1311 species, 22.6 per cent) and numbers from China range from 100 to 400 (Pyšek, Pergl, et al., 2017). Western Asia is comparatively poor in numbers of alien plants (**Table 2.25**; Pyšek, Pergl, et al., 2017).

Table 2.25. Top most widespread invasive alien species for Asia and the Pacific

The number of regions where the species has been recorded and classified as being invasive based on GRIIS (Pagad et al., 2022). Note this table only refers to the distribution of invasive alien species rather than their impacts which are covered in **Chapter 4.** A maximum of three species is shown for each group (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species

according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species name	No. of regions	Species name	No. of regions
Mammals		**Molluscs**	
Rattus rattus (black rat)	23	*Lissachatina fulica* (giant African land snail)	15
Mus musculus (house mouse)	18	*Pomacea canaliculata* (golden apple snail)	11
Rattus norvegicus (brown rat)	14	*Euglandina rosea* (rosy predator snail)	6
Birds		**Crustaceans**	
Acridotheres tristis (common myna)	16	*Amphibalanus improvisus* (bay barnacle)	3
Columba livia (pigeons)	7	*Cherax quadricarinatus* (redclaw crayfish)	3
Corvus splendens (house crow)	7	*Procambarus clarkii* (red swamp crayfish)	3
Fishes		**Vascular plants**	
Gambusia holbrooki (eastern mosquitofish)	16	*Lantana camara* (lantana)	29
Cyprinus carpio (common carp)	15	*Pontederia crassipes* (water hyacinth)	28
Gambusia affinis (western mosquitofish)	12	*Leucaena leucocephala* (leucaena)	23
Reptiles		**Algae**	
Hemidactylus frenatus (common house gecko)	4	*Alexandrium minutum* (dinoflagellate)	2
Iguana iguana (iguana)	4	*Caulerpa taxifolia* (killer algae)	1
Trachemys scripta elegans (red-eared slider)	4	*Chattonella marina* (raphidophyte)	1
Amphibians		**Bryophytes**	
Lithobates catesbeianus (American bullfrog)	6		
Rhinella marina (cane toad)	6	**Fungi**	
Xenopus laevis (African clawed frog)	2	*Pyrrhoderma noxium*	4
Insects		*Amanita muscaria* (fly agaric)	1
Solenopsis geminata (tropical fire ant)	14	*Austropuccinia psidii* (myrtle rust)	1
Tapinoma melanocephalum (ghost ant)	14	**Oomycetes**	
Brontispa longissima (coconut hispine beetle)	13	*Phytophthora cinnamomi* (Phytophthora dieback)	3
Arachnids		**Bacteria and protozoans**	

Aculops lycopersici (Tomato russet mite)	1	*Vibrio cholerae* (cholera)	3
Latrodectus geometricus (brown widow spider)	1	*Yersinia pestis* (black death)	1
Latrodectus hasselti (Redback spider)	1		

2.4.4.3. Microorganisms

Trends

In general, information on the trends of alien microorganisms in Asia is very scarce as for other IPBES regions. Data from China indicate that of the 27 invasive alien fungi recorded so far, only two new additions were reported after the year 2000 (H. G. Xu & Qiang, 2018). In India, only one new invasive alien fungal pathogen (*Puccinia horiana* (white rust of chrysanthemum)) has been recorded in the last five years (Akhtar et al., 2019; Dubey et al., 2021). However, 15 invasive fungal pathogens were intercepted by plant quarantine (Akhtar et al., 2019, 2021; Dubey et al., 2021) between 2015 and 2020. Only scattered information on trends of invasive alien fungi is available from other countries in Asia.

Status

Twenty-seven invasive alien fungal pathogens were recorded from China (H. G. Xu & Qiang, 2018), 21 from India (Akhtar et al., 2019, 2021; Dubey et al., 2021; Government of India, 2005), 30 from the Maldives (Shafia & Saleem, 2003), and 15 from the Lao People's Democratic Republic (Nhoybouakong & Khamphouke, 2003). Further information on invasive alien fungi is not traceable or available from countries in Asia though it is clear from studies by Fisher et al. (2020) that several new invasive alien fungi may have been introduced from across the globe.

A comparatively high number of known alien macrofungi has been reported for Asia and the Pacific which harbours at least 235 established alien species (Monteiro et al., 2020). Most of these alien species belong to the order Agaricales (54 per cent), followed by Boletales (21 per cent), and Russulales (10 per cent). The most widespread alien macrofungi is *Pyrrhoderma noxium*. The countries with the highest numbers of known alien macrofungi are New Zealand (170 species) and Australia (40 species). This highlights the paucity of knowledge on invasive alien microparasites in this region. In general, it is assumed that goods, species including humans constantly carry a multitude of microorganisms around the globe and that many of them are introduced every year without detection.

2.4.4.4. Islands

Many islands in the Asia-Pacific region are significantly impacted by invasive alien species (IPBES, 2018b). For example, French Polynesia has undergone severe invasions by species ranging from avian malaria, plants, mammals, ants, birds, and predatory land snails (Brodie et al., 2014; Howarth, 1985; J.-Y. Meyer, 2014; J.-Y. Meyer & Butaud, 2009). Mammals are widely introduced on islands in Asia and the Pacific (Courchamp et al., 2003), with examples including commensal rodents (mice, black rats, brown rats, and Pacific rats), rabbits, pigs, goats, cats, and foxes, in particular on many islands (D. J. Campbell & Atkinson, 2002; Priddel et al., 2000; Reaser et al., 2007; St Clair, 2011; Towns et al., 2006).

Conversely, while some islands are invaded by only a few alien species, they are archetypal examples of island invasions. Invasive *Herpestes* sp. (mongooses) have been introduced on the

Japanese islands of Amami-Oshima and Okinawa (Goldson, 2011; Reaser et al., 2007; The Ministry of the Environment of Japan, 2014). On Guam, *Boiga irregularis* (brown tree snake) has spread widely reaching densities in excess of 31,000 individuals per km^2 (CGAPS, 1997; Fritts & Rodda, 1998; Rogers et al., 2017). On Guam and on Christmas Island, *Anoplolepis gracilipes* (yellow crazy ant) invasions were boosted by the invasive *Tachardiaephagus tachardiae* (yellow lac scale insect), which supplies yellow ants with honeydew (O'Dowd et al., 2003; Reaser et al., 2007). Other typical examples are gastropod invasions on many Polynesian islands, such as *Lissachatina fulica* (giant African land snail; Tsatsia & Jackson, 2022). Invasive plants are also a serious issue on many Asia-Pacific islands, such as Tahiti (J.-Y. Meyer & Florence, 1996), Lord Howe Island (T. D. Auld & Hutton, 2004), and Carnac Island (Abbott et al., 2000), while invasive soilborne plant pathogens, such as the fungus *Phytophthora cinnamomi* (Phytophthora dieback), are problematic in over 70 countries including several Australian islands (T. D. Auld & Hutton, 2004; Pickering et al., 2007), Fiji, Samoa, Tuvalu, and New Zealand (e.g., F. Campbell, 2010; Thaman, 2011; Thaman & O'Brien, 2011). Hawaii is another classic example of an archipelago heavily invaded by many species groups, being among the three regions with the most established alien species in the world (Dawson et al., 2017): over 1,000 plants (W. L. Wagner et al., 1999), 3,000 arthropods (Nishida, 2002), and 110 vertebrates (Moulton & Pimm, 1983; Vitousek et al., 1987).

Pacific Islands are widely invaded by alien birds with New Zealand being a global hotspot of alien bird richness. More than 130 species were introduced to New Zealand, mostly deliberately by acclimatization societies set up by British colonists. More than 30 species are now established, including dense populations of several passerine species imported from Britain, such as *Turdus philomelos* (song thrush), *Turdus merula* (Eurasian blackbird), *Prunella modularis* (dunnock), *Chloris* sp. (greenfinch), *Acanthis* sp. (redpoll) and *Emberiza citrinella* (yellowhammer).

2.4.4.5. Knowledge and data gaps

For alien plants, Asia and the Pacific have lower data coverage than other continents; data are available on established alien species for 68.5 per cent of the area of tropical Asia as a whole (Pyšek, Pergl, et al., 2017; van Kleunen et al., 2015). Notable exceptions represent some well-studied invasion hotspots such as Australia, New Zealand and Hawaii (van Kleunen et al., 2015, 2019; **Figure 2.6**). Mainland Asia is a region especially affected by knowledge gaps for alien mammals, likely due to a low sampling effort (Pyšek et al., 2008) and/or linguistic barriers (Angulo et al., 2021). Notably, while reports of alien mammals in Hong Kong, Special Administrative Region of China, are numerous and exhaustive, very little information is available in English for mainland China (Biancolini et al., 2021). However, the situation has improved recently with several specialized accounts published or underway (Dorjee et al., 2020; Inderjit et al., 2018; Patzelt et al., 2022), and this trend is expected to continue. Temporal information such as first records is generally scarce for most regions in Asia and the Pacific.

The completeness of the information about alien amphibians and reptiles and freshwater species in Asia and the Pacific varies substantially by country. While some countries in North-East Asia and Oceania are relatively well-studied, others, particularly in southeast Asia and western Asia, have substantial knowledge gaps (Capinha et al., 2017; Chapple et al., 2016; C. Chen et al., 2017; Cogălniceanu et al., 2014; Das, 2015; Kraus, 2009; Lee et al., 2019; Rights and Resources Initiative, 2015; Seebens, Blackburn, et al., 2017; Soorae et al., 2010; Van Wilgen et al., 2010; Zug, 2013). In addition, further genetic work is needed to resolve the status of various species and populations of alien reptiles throughout the Pacific and western Asia (Cogălniceanu et al., 2014; Zug, 2013).

The total number of marine alien species varies among studies, in part due to a lack of standardized terminology, sampling methods, environments studied, and taxonomic expertise available to assess species lists and record dates (Marchini et al., 2015). For example, many species counted as marine

alien species in the northwest Pacific are present in aquaculture facilities, while it remains unknown whether they have established in some cases. Some assessment lists only include species detected on vectors, some others consider different delineations of marine regions, while yet others are country specific.

Asia and the Pacific is grossly under-explored for alien fungi and other microorganisms. The high number of alien macrofungal records in New Zealand and Australia are likely influenced by high research and sampling intensities in these regions. Much less data and fewer studies on alien macrofungi are available for most other countries in Asia and the Pacific.

2.4.5. Trends and status of alien and invasive alien species in Europe and Central Asia

This section reports on the trends and status of alien species of Europe and Central Asia for animals (**section 2.4.5.1**), plants (**section 2.4.5.2**), microorganisms (**section 2.4.5.3**) and islands (**section 2.4.5.4**), and provides an overview of data and knowledge gaps (**section 2.4.5.5**). A description of IPBES regions and sub-regions including a spatial representation is provided online (IPBES Technical Support Unit On Knowledge And Data, 2021) and in **Chapter 1**, **section 1.6.4**.

2.4.5.1. Animals

Trends

The number of alien animal species in Europe and Central Asia has increased across various taxonomic groups including vertebrates (Rabitsch & Nehring, 2017), insects (Roques et al., 2016), molluscs (Peltanová et al., 2012) and freshwater species (Muñoz-Mas & García-Berthou, 2020; Nunes et al., 2015). Comparisons of long-term trends among sub-regions show much larger numbers of alien species recorded for Central and Western Europe, which has the highest numbers of alien species for all animal groups and at all times, compared to other sub-regions (**Figure 2.33**). While rates of increase remained relatively constant over the last 200 years for alien mammals, they rose sharply in recent decades for birds and invertebrates. Rates of increase of alien species remained relatively constant for all groups in Eastern Europe, but available numbers in Central Asia are often too low to assess trends (**Figure 2.33**).

Alien mammal introductions first occurred in Europe and Central Asia during prehistoric times, with major introductions from Asia to Europe and from the mainland to islands (Biancolini et al., 2021; Long, 2003). The spread of agriculture brought domestic species (e.g., *Capra hircus* (goats), *Ovis aries* (sheep), *Felis catus* (cat)), while island colonization by humans brought game species (e.g., *Lepus europaeus* (European hare), *Glis glis* (European edible dormouse), *Oryctolagus cuniculus* (rabbits)) as well as stowaways (*Apodemus sylvaticus* (long-tailed field mouse), *Crocidura suaveolens* (lesser white-toothed shrew), *Microtus arvalis* (common vole)) (Biancolini et al., 2021; Long, 2003). Biological invasions of islands intensified with the growth of the sea trade in the following centuries causing the disappearance of many natural island ecosystems, especially in the Mediterranean basin (Masseti, 2009). Hunting has always been and continues to be a major pathway for alien mammals and birds on both the mainland and the islands of Europe and Central Asia (Genovesi et al., 2012; Monaco et al., 2016).

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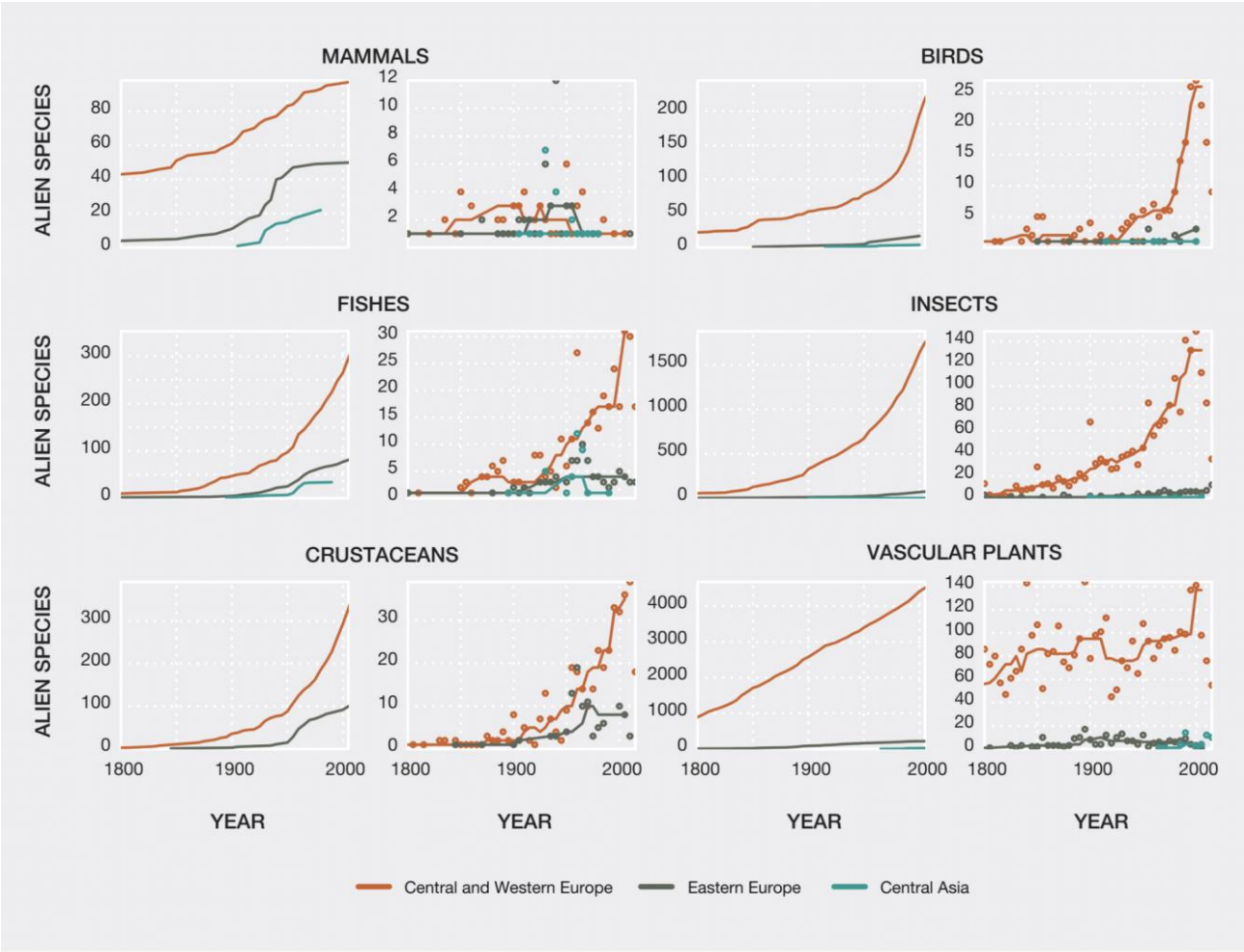

Figure 2.33. Trends in numbers of established alien species in Europe and Central Asia. Cumulative numbers (left panels) and number of established alien species per five-year intervals (right panels). Numbers underestimate the actual extent of alien species occurrences due to a lack of data. Lines in right panels indicate smoothed trends calculated as running medians (**section 2.1.4** for further details about data sources and data processing). Note that presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Europe and Central Asia has experienced a growing number of alien reptile and amphibian introductions, a trend that will likely continue (Seebens, Bacher, et al., 2021; Seebens, Blackburn, et al., 2017). Trends in alien reptiles and amphibians follow a similar pattern: historical events and trade routes around the Mediterranean Basin have resulted in some of the oldest known introductions of alien amphibians and reptiles in the world occurring in this region (Mateo et al., 2011; Pleguezuelos, 2002). In line with global trends, the number of alien amphibians and reptiles has increased in this region and the pet trade is expected to contribute more species in the near and medium futures (Capinha et al., 2017; Filz et al., 2018; Kraus, 2009; Mateo et al., 2011).

Introductions of alien freshwater animals increased after the mid-nineteenth century due to the activities of acclimatization societies, mainly for angling (Gherardi et al., 2009). Established alien species numbers also increased notably after World War II due to more intensive trade, openings of major inland canals and waterways in Central and Western Europe, and the intensification of aquaculture (Gherardi et al., 2009; Nunes et al., 2015). The main pathways of introduction were releases and escapes through aquaculture, deliberate stocking, and pet and aquarium trades. The latter acquired more importance as a driver facilitating introductions since the 1990s (Nunes et al., 2015). In central and north-eastern Europe, interconnected canals and waterways were the main pathways of introduction, while in Central and Western Europe releases and escapes are linked to aquaculture and pet and aquarium trades. A slight decrease in introduction rates in recent decades has been reported on the Iberian Peninsula (Muñoz-Mas & García-Berthou, 2020). Alien species introductions are further assisted by unintentional translocations, such as the opening of waterways in Israel (Goren & Ortal, 1999).

Across the coastal areas of Europe, the number of detections and introductions of alien species has increased over time, although numbers differ among assessments (Bailey et al., 2020; Gollasch, 2006; Katsanevakis et al., 2020; Tsiamis et al., 2019), especially for the eastern Mediterranean Sea since the earliest inventories taken during the 1960s (Galil et al., 2021b). For example, the number of marine alien species along the coast of Israel has increased three-fold from 1970 (147 alien species) to 2020 (452 alien species), and this trend is consistent as new alien species detections still appear in the scientific literature. For the Baltic Sea, the annual introduction rate has more than doubled since 1950: 1.4 species per year between 1950 and 1999 and 3.2 between 2000 and 2018 (ICES, 2019).

Status

Currently 85 alien mammals are known to be established in Europe and Central Asia, from 7 orders and 24 families (Biancolini et al., 2021). The most numerous orders are Rodentia (26 species), Cetartiodactyla (24), Carnivora (18) and Eulipotyphla (8). Alien mammal hotspots are present in Central and Western Europe, numerous Mediterranean islands, the British Isles, Italy, Scandinavia, Eastern Europe and European Russia (Biancolini et al., 2021). Most alien mammals are native to other parts of Europe and Central Asia (42) and the major outside donor is Asia and the Pacific (14), followed by the Americas (10), and Africa (4). This great reshuffling of mammal fauna was mainly driven by hunting (36 cases), pet trade (22), stowaway transportation (16), intentional introductions (12), conservation purposes (11) and fur exploitation (11) (Biancolini et al., 2021). For example, squirrels were released or escaped from captivity in the last several decades, creating numerous alien populations scattered across Europe (Biancolini et al., 2021). A well-known example is *Sciurus carolinensis* (grey squirrel), which was introduced to the United Kingdom and Italy (Bertolino et al., 2008, 2014; Gaertner et al., 2016). *Ondatra zibethicus* (muskrat), *Nyctereutes procyonoides* (raccoon dog), and *Mustela vison* (American mink) are among the most widespread species in Europe and Central Asia (Biancolini et al., 2021; Genovesi et al., 2012; Tedeschi et al., 2022).

Many alien bird species were introduced during European colonial expansion including a large number introduced to Europe. Game and ornamental species were particularly popular, such that Europe now has populations of a number of alien galliforms and wildfowl. Other such introductions pre-date colonialism, such as *Phasianus colchicus* (common pheasant), which is widespread in Europe and still released in various countries every year by the tens of millions. Prior to the bird flu epidemic of 2005, Europe was a major hub for the caged bird trade, but European Union-wide bans on imports have greatly restricted the influx of species from outside the continent (Reino et al., 2017). There is still extensive trade in captive-bred birds within Europe, and escapes continue to threaten further alien species introductions. The caged bird trade is the major source of alien species in Asia, notably in trade hubs in the Far East. Millions of birds continue to be trapped from wild populations in Asia, and pose a substantial extinction threat to popular species, as well as a risk of new alien populations.

Table 2.26. Numbers of established alien species for subregions of Europe and Central Asia

For mammals, birds, and vascular plants ranges of values indicate variation among databases (**section 2.1.4** for further details about data sources and data processing). Note presented numbers may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this table is available at https://doi.org/10.5281/zenodo.7615582

	Central and Western Europe	Central Asia	Eastern Europe	Total
Mammals	64-133	5-23	24-80	72-164
Birds	218-627	4-5	20-24	221-630
Fishes	423	51	119	469
Reptiles	94	0	6	98
Amphibians	42	2	5	43
Insects	2,698	28	213	2,747
Arachnids	289	2	6	289
Molluscs	557	4	75	584
Crustaceans	420	10	88	563
Vascular plants	4,498-7,896	134-361	1,950-2,400	5,146-8,519
Algae	483	0	82	526
Bryophytes	23	0	1	23
Fungi	594	3	28	609
Oomycetes	59	0	2	59
Bacteria and protozoans	22	0	2	23
Total	12,711-16,587	265-511	2,903-3,413	11,472-15,346

Europe and Central Asia have several global hotspots of alien amphibians and reptiles. These include the Balearic Islands (20 species), mainland Spain (13 species), mainland Italy (11 species), mainland France (10 species), and the United Kingdom (10 species) (Capinha et al., 2017; Ficetola et al., 2010; Kark et al., 2009; Kraus, 2009; Mateo et al., 2011). Fewer alien reptiles and amphibians have been reported from Central Asian countries than in Europe (Capinha et al., 2017; Kraus, 2009).

According to Nunes et al. (2015), there are 534 alien freshwater animals (46 per cent native to some European areas) in Europe and Central Asia. The Iberian Peninsula, France, Italy, the United Kingdom, and Germany host the highest numbers of species (Gollasch & Nehring, 2006; R. P. Keller et al., 2009; Muñoz-Mas & García-Berthou, 2020; Nunes et al., 2015; Teletchea & Beisel, 2018). For Uzbekistan, 31 alien freshwater fishes have been recorded (Yuldashov, 2018). Most introduced fish arrived mainly through stocking, aquaculture, or pet and aquarium trades, followed by crustaceans and molluscs, both mainly via ornamental trade and through corridors (e.g., canals and waterways; Muñoz-Mas & García-Berthou, 2020; Nunes et al., 2015). Some species, such as *Cyprinus carpio* (common carp), *Sander lucioperca* (pike-perch), *Silurus glanis* (wels catfish) or Ponto-Caspian gobies, are only native to parts of western Europe but have now established in much of European fresh waters (e.g., Leprieur et al., 2008). Similarly, many widespread species such as *Perca fluviatilis* (perch), *Rutilus rutilus* (roach) or *Alburnus alburnus* (bleak) are not native to the peninsulas in southern Europe, which have distinct, threatened fish faunas with high endemism (Yuldashov, 2018).

2.4.5.2. Plants

Trends

Since the start of the nineteenth century, Central and Western Europe has had a steady increase in alien plant introductions and data indicate no deceleration of this trend (**Figure 2.33**). First records for Eastern Europe and Central Asia show very slow increases, partly due to lower research effort in these regions relative to Central and Western Europe (**section 2.4.5.5**). A recent Europe-wide inventory of established alien plants, including Central and Western, and a portion of Eastern Europe was conducted through the project Delivering Alien Invasive Species In Europe (Lambdon et al., 2008) and recorded 4,139 established alien plant taxa (Pyšek, Pergl, et al., 2017; van Kleunen et al., 2015), an increase of 390 taxa (or 9.6 per cent). The introduction of alien aquatic plants increased after 1950, the main pathway being the ornamental trade, followed by cultivation and contaminants of commodities (Nunes et al., 2015). Ornamental trade and cultivation had similar rates in different European areas while contaminants of commodities were mostly recorded in southern Europe (Nunes et al., 2015). The number of alien aquatic plant species is still relatively low in European freshwaters but is sharply increasing, having doubled in nearly 30 years (Hussner et al., 2010).

Status

In Central and Western Europe, a total of 8,565 alien vascular plants, 497 established alien algae, and 25 established alien bryophytes have been recorded (**Table 2.27**). The GloNAF database reports 4139 established alien vascular plants (Pyšek, Pergl, et al., 2017; van Kleunen et al., 2015). The highest numbers of established alien plants are recorded in England (1,379), Sweden (874), Scotland (861), Wales (835), France (716), Norway (595), Belgium (508), Italy (478), Spain (454), and Germany (451) indicating that the northern part of the continent, particularly United Kingdom, Ireland, and Scandinavia are heavily invaded by established alien species. Only a few regions in Eastern Europe (perhaps due to lack of data) harbour comparably high numbers of established alien species, such as the European part of Russia (649), Ukraine (626) and Bulgaria (593) (Pyšek, Pergl, et al., 2017; van Kleunen et al., 2015, 2019). Some of these countries also have the highest per centage of established alien species as a proportion of the total flora. In England, established alien species make up 47 per cent of the total flora, in Wales 44 per cent, Scotland 42 per cent, Sweden 35 per cent, in Norway 32 per cent, and in the European part of Russia 37 per cent (Pyšek, Pergl, Dawson, et al., 2020). There are 35 alien species that have become established in more than 30 regions of Europe, that is, at least half of the European regions considered in the GloNAF database, the most widespread being *Erigeron canadensis* (Canadian fleabane; recorded in 76 per cent of regions), *Elodea canadensis* (Canadian pondweed), *Matricaria discoidea* (rounded chamomile),

Oenothera biennis (common evening primrose), *Solidago canadensis* (Canadian goldenrod) and *Galinsoga parviflora* (gallant soldier) (**Table 2.27**). Central Asia is generally less invaded by alien plants with country floras in this region harbouring 50–70 established alien species which corresponds to 1.9–4.5 per cent contribution to total plant diversity (Pyšek, Pergl, et al., 2017).

According to Nunes et al. (2015), there are 210 alien freshwater plants (38 per cent native to some European areas). Hussner (2012) found that the highest number of alien plant species in all of Europe is reported for Italy and France, followed by Germany, Belgium, Hungary, and the Kingdom of the Netherlands. The most frequently introduced plants are the angiosperms: 200 out of 210 (Nunes et al., 2015).

Over last decade, negative impacts associated with the spread of particular alien aquatic plant species (e.g., *Elodea* spp. (waterweeds), *Pontederia crassipes* (water hyacinth), *Ludwigia* spp. (primrose-willow), *Hydrocotyle ranunculoides* (floating pennywort), *Myriophyllum aquaticum* (parrot's feather)) increased in Europe (Hussner, 2012). Even though the number of alien aquatic plants appears relatively small compared to alien terrestrial plant species, the European and Mediterranean Plant Protection Organization (EPPO, 2021) has listed 18 of these species as invasive or potentially invasive within the European and Mediterranean Plant Protection Organization's region covering most of Europe and parts of Central Asia and North Africa. In total, 96 aquatic alien species from 30 families have been reported as established alien species from at least one European country. Sixteen alien species belong to the family of Hydrocharitaceae, followed by the Nymphaeaceae and Lemnaceae (both with nine plant species). Most aquatic alien plant species introduced into Europe are native to North America (26 per cent) and Asia (29 per cent) (Hussner, 2012). The highest number of aquatic alien plant species was found in Italy (34 species), France (34 species), Germany (27), Belgium, and Hungary (both 26), and was lowest in the Balkan region and the northern and eastern parts of Europe (Hussner, 2012). *Elodea canadensis* (Canadian pondweed) is the most widely distributed alien aquatic plant in Europe, occurring in 41 European countries (but not in Cyprus, Malta, Iceland, Greece, and Montenegro). *Azolla filiculoides* (water fern) is the second most widely distributed species (25 countries), followed by *Vallisneria spiralis* (eelweed) (22) and *Elodea nuttallii* (Nuttall's waterweed) (20) (Hussner, 2012).

Table 2.27. Top most widespread invasive alien species for Europe and Central Asia

The number of regions where the species has been recorded and classified as invasive based on GRIIS (Pagad et al., 2022). Note this table refers only to the distribution of invasive alien species rather than their impacts which are covered in **Chapter 4**. A maximum of three species is shown for each group (see **section 2.1.4** for further details about data sources and data processing). "No. of regions" denotes the number of regions with confirmed occurrences of that species according to the chapter database. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

Species name	**No. of regions**	**Species name**	**No. of regions**
Mammals		**Molluscs**	
Mustela vison (American mink)	15	*Dreissena polymorpha* (zebra mussel)	15
Rattus norvegicus (brown rat)	11	*Corbicula fluminea* (Asian clam)	13
Myocastor coypus (coypu)	10	*Potamopyrgus antipodarum* (New Zealand mudsnail)	13
Birds		**Crustaceans**	
Alopochen aegyptiaca (Egyptian goose)	8	*Pacifastacus leniusculus* (American signal crayfish)	18

Branta canadensis (Canada goose)	7	*Amphibalanus improvisus* (bay barnacle)	14
Psittacula krameri (rose-ringed parakeet)	6	*Faxonius limosus* (Spiny-cheek crayfish)	14
Fishes		**Vascular plants**	
Pseudorasbora parva (topmouth gudgeon)	19	*Ailanthus altissima* (tree-of-heaven)	32
Lepomis gibbosus (pumpkinseed)	18	*Robinia pseudoacacia* (black locust)	31
Gambusia holbrooki (eastern mosquitofish)	15	*Solidago canadensis* (Canadian goldenrod)	26
Reptiles		**Algae**	
Trachemys scripta (pond slider)	6	*Sargassum muticum* (wire weed)	7
Trachemys scripta elegans (red-eared slider)	4	*Coscinodiscus wailesii* (diatom)	5
Chelydra serpentina (common snapping turtle)	2	*Bonnemaisonia hamifera* (red algae)	4
Amphibians		**Bryophytes**	
Lithobates catesbeianus (American bullfrog)	7	*Campylopus introflexus* (heath star moss)	10
Pelophylax ridibundus (Eurasian marsh frog)	3	*Orthodontium lineare* (cape thread-moss)	2
Triturus carnifex (Italian crested newt)	3	**Fungi**	
Insects		*Ophiostoma novo-ulmi* (Dutch elm disease)	9
Cameraria ohridella (horsechestnut leafminer)	13	*Hymenoscyphus fraxineus* (ash dieback)	5
Harmonia axyridis (harlequin ladybird)	12	*Ophiostoma ulmi* (Dutch elm disease)	4
Leptinotarsa decemlineata (Colorado potato beetle)	8	**Oomycetes**	
Arachnids		*Aphanomyces astaci* (crayfish plague)	13
Opilio canestrinii (harvestman)	3	*Phytophthora cambivora* (root rot of forest trees)	3
Varroa destructor (Varroa mite)	3	*Phytophthora ramorum* (sudden oak death)	3
Mermessus trilobatus (trilobate dwarf weaver)	2	**Bacteria and protozoans**	
		Anabaenopsis raciborskii (cyanobacteria)	1
		Erwinia amylovora (fireblight)	1

2.4.5.3. Microorganisms

Trends

Due to global trade of live plants and animals, the rate of introduction of alien fungi, oomycetes, and other microorganisms to Europe and Central Asia is likely to further accelerate (Hulme, 2021). Several fungi, oomycetes, and other microorganisms causing diseases have been introduced in recent decades (Nunes et al., 2015). For example, within the past 20 years, 5 downy mildew pathogens with the potential to cause significant losses have been introduced to Europe (Gilardi et al., 2013; Görg et al., 2017; Thines, 2011; Thines et al., 2020; Voglmayr et al., 2014). These organisms were most likely introduced with seeds or latently infected plants, making clear the necessity for better quarantine procedures for alien plants and for local production of plants and seeds whenever possible.

Status

Europe and Central Asia has a well-documented history of biological invasions by alien plant and animal parasitic fungi and oomycetes. Well-known examples are *Batrachochytrium dendrobatidis* (chytrid fungus; Longcore et al., 1999), *Aphanomyces astaci* (crayfish plague; Mrugała et al., 2015), *Phytophthora infestans* (Phytophthora blight; Yoshida et al., 2013), and *Plasmopara viticola* (grapevine downy mildew; Gessler et al., 2011). In addition, alien species have also invaded Europe as saprotrophsor symbionts, but the few documented examples such as *Clathrus archeri* (devil's fingers) are likely only the tip of the iceberg (Desprez-Loustau et al., 2007; Litchman, 2010).

In Europe and Central Asia, the highest numbers of invasive alien forest pathogenic fungi are reported from the central-southern region (e.g., France, Italy, and Switzerland; Santini et al., 2013). For example, *Phytophthora ramorum* (sudden oak death), which has had significant impacts on native forests, is thought to have been introduced to the United Kingdom via the ornamental plant trade (Jung et al., 2021). Most forest pathogenic fungi are native to the northern hemisphere, but about one third are of unknown origin (Desprez-Loustau, 2009). The incidence in Europe of alien powdery mildews (Erysiphales) is higher in terms of expected species numbers and this may reflect responses to climate change in a group adapted for long-distance aerial spore dispersal (Heluta et al., 2009). Using dried reference collection samples, Gross et al. (2021) demonstrated that three species of *Erysiphe* could be linked to the incidence of powdery mildew in oaks, a disease that emerged in Europe at the beginning of the twentieth century. By comparison, the incidence of specialized alien insect parasites of the order Laboulbeniales is comparatively low given their high species numbers (Desprez-Loustau, 2009). More aggressive genotypes of known plant pathogenic fungi may also arrive and become invasive (Arenz et al., 2011). Alien and invasive microfungi pathogenic to animals include *Batrachochytrium dendrobatidis* (chytrid fungus), which is the agent of chytridiomycosis, a disease spread by trade and causing massive amphibian declines worldwide (Weldon et al., 2004), and *Pseudogymnoascus destructans* (white-nose syndrome fungus) in bats (Thakur et al., 2019).

Among all IPBES regions, Europe and Central Asia represents the region with the best available knowledge on the distribution of alien macrofungi with several national lists of alien fungi available (e.g., Desprez-Loustau et al., 2010; Motiejūnaitė et al., 2016). However, information for the Central Asian and Eastern European sub-regions, is much scarcer, and the absence or low number of alien macrofungi as known for these regions is likely a clear underestimation of actual numbers.

2.4.5.4. Islands

Mediterranean islands are biodiversity hotspots and have been invaded by large numbers of alien plant and animal species for centuries, many of which are now established (e.g., Capizzi, 2020;

Chainho et al., 2015; Ruffino et al., 2009). Many North Sea and Baltic Sea islands have also been invaded, for example by *Mustela vison* (American mink) (e.g., Bonesi & Palazon, 2007). Islands belonging to Europe include overseas territories in most oceans. In particular, the United Kingdom and France have many islands in the southern Atlantic and in the Pacific. Biological invasions on islands related to European countries may be due to proximity of continents (islands off the Atlantic and Channel Sea coasts) or the colonization of more remote islands (e.g., French Polynesia and New Caledonia). Among the most studied taxa, the mammals of these islands, such as Gough Island, Crozet Island, or the Kerguelen Islands include rats, mice, cats, cattle, and mouflons (Davies et al., 2015; C. W. Jones et al., 2019; Pascal, 1980).

2.4.5.5. Data and knowledge gaps

While sampling and reporting intensity is high for alien mammals in Western Europe, data coverage and quality decrease eastward towards Eastern Europe, including Russia (Biancolini et al., 2021). Significantly fewer sources of information are available for these areas in comparison to Western Europe and reports frequently lack extensive details on alien species trends, ecology, distribution, and impacts. This could reflect linguistic barriers that hinder data sharing (Angulo et al., 2021) as the available literature published in English with respect to Eastern Europe cites numerous works written in other languages (e.g., Russian) (Khlyap et al., 2011). A similar situation is reported for freshwater species, which are well reported for Europe, especially Western Europe (Nunes et al., 2015), while less data are available for Central Asia.

While information available on alien amphibians and reptiles in this IPBES region has been thoroughly collected (Capinha et al., 2017; Kark et al., 2009; Kraus, 2009), some countries in Western Europe and Central Asia have been understudied and those lists of alien amphibians and reptiles are likely incomplete (Capinha et al., 2017; Seebens, Blackburn, et al., 2017; N. J. van Wilgen et al., 2018).

Europe is amongst the best-researched continents for plant invasions (Pyšek, Hulme, et al., 2020) and many regions in Central and Western Europe possess high quality data compared to other parts of the world (Lambdon et al., 2008; Pyšek, Blackburn, et al., 2017; Pyšek, Pergl, Dawson, et al., 2020). Many countries have specialized catalogues and inventories with information going beyond the distribution of alien species (e.g., Celesti-Grapow et al., 2009; E. J. Clements & Foster, 1994; Essl & Rabitsch, 2002; Klotz et al., 2003; Preston et al., 2002, 2004; Pyšek et al., 2002; S. C. P. Reynolds, 2002). For Eastern Europe, there are data gaps and incomplete species lists for several countries including a large part of Russia (van Kleunen et al., 2015, 2019). Work is currently underway to close this data gap (e.g., Leostrin & Pergl, 2021; Vinogradova et al., 2018), and more species are likely to be identified as established alien species in Europe. Some countries in Central Asia also lack inventories (appendix 1 in Pyšek, Blackburn, et al., 2017).

2.5. Trends and status of alien and invasive alien species by IPBES units of analysis

This section reports on the temporal trends and status of the distribution of alien and invasive alien species for each IPBES unit of analysis. IPBES units of analysis represent a broad-based global classification system considering both the state of nature in classes, equivalent to biomes, and in anthropogenically-altered biomes or "anthromes". The units correspond broadly to global classifications of nature and human interactions, serving the need for analysis and communication in a global policy context. More details about the units of analysis are provided in **Chapter 1**, **section 1.6.5** and online (IPBES, 2019b). The following section is sub-divided into an overview (**section 2.5.1**), terrestrial (**section 2.5.2**), freshwater (**section 2.5.3**), and marine (**section 2.5.4**) units of analysis as well as anthroponized areas (**section 2.5.5**).

2.5.1. Overview of trends and status by IPBES units of analysis

While no studies on biological invasion dynamics among comparative units of analysis exist, some studies have investigated patterns using similar delineations of study regions such as freshwater, marine, and terrestrial habitats. In general, far more studies are available for terrestrial alien species (although availability varies for above- and belowground) than for marine and freshwater systems. For instance, one comprehensive global analysis of first records of established alien species shows that 64 per cent of all studies had an explicit focus on terrestrial habitats, 13 per cent addressed marine and 12 per cent freshwater habitats, and the remaining were cross-taxonomic (Seebens, Blackburn, et al., 2017). As a result, most established alien species have been reported from terrestrial habitats (over 75 per cent), while freshwater or marine alien species numbers are both of similarly low range (less than 10 per cent). Terrestrial alien species invasions were usually recorded earlier in time compared to freshwater species, which in turn were reported earlier than marine species (Zieritz et al., 2017). Likewise, before 1840 most (about 75 per cent) established alien species recorded in north-western Europe represented terrestrial species, and the proportion has dropped continuously to less than 20 per cent more recently (Zieritz et al., 2017). Only a few studies compared the trends and status of alien species across terrestrial, freshwater, and marine habitats at large spatial scales (e.g., Roy, Peyton, et al., 2014; Sandvik, Dolmen, et al., 2019; H. Xu et al., 2012; Zieritz et al., 2017). Other studies reported similar increases in established alien species across terrestrial, marine, and freshwater habitats with a tendency of freshwater alien species numbers accelerating more rapidly in recent years (O'Flynn et al., 2014; Roy, Preston, et al., 2014; H. Xu et al., 2012).

2.5.2. Trends and status of alien and invasive alien species in terrestrial units of analysis

Box 2.7. **Mountain regions: A global assessment of trends and status of alien and invasive alien species**

Elevational patterns of plant invasions have been described for many mountain regions around the world and with very few exceptions, established alien species richness peaks at lower elevations and declines towards the highest elevations, closely following patterns of human settlements and disturbance (e.g., Alexander et al., 2011; Fuentes-Lillo et al., 2021; Haider et al., 2010; Pauchard et al., 2009; Pérez-Postigo et al., 2021; Tanaka & Sato, 2016). Most introduced alien species are pre-adapted to the environmental conditions at low elevations and need a broad environmental tolerance to spread towards high mountain sites (Alexander et al., 2011). Therefore, alien species at high elevations are typically environmental generalists, and only rarely are mountain specialist species directly introduced at high elevations (Alexander et al., 2016; Steyn et al., 2017). As the regional lowlands are the most important source of alien plants found at high elevations, alien mountain floras are surprisingly dissimilar across mountain ranges and continents. In a study analyzing alien

species lists from 13 mountain regions, about 60 per cent of alien species were recorded in a single mountain area, and less than 5 per cent were found in more than half of the regions included in the study (McDougall et al., 2011).

Anthropogenic corridors such as roads, trails, and railways strongly facilitate the spread of alien plants from low to high elevations (Alexander et al., 2011; Lembrechts et al., 2017; Liedtke et al., 2020; Rashid et al., 2021; M. Yang et al., 2018), and alien plants are much more common in disturbed habitats directly adjacent to such corridors compared to more remote natural habitats (Seipel et al., 2012). Thus far, few alien species have been able to penetrate natural communities, especially at higher elevations, but those that have invaded are often shade and moisture tolerant (McDougall et al., 2018).

While there is no evidence that alien species in mountains have caused the local extinction of native species, they have a strong impact on multiple dimensions of biodiversity (B. W. van Wilgen et al., 2020). First, they reduce differences in community composition between low and high elevations, and thus negatively affect beta-diversity, leading to a biotic homogenization in mountains – and in the long-term maybe also across mountain regions. A global study based on a standardized vegetation survey demonstrated that alien species along roadsides either shifted the richness peak of native plants to lower elevations, or even changed the shape of the relationship between native species richness and elevation (Haider et al., 2018).

In the last 15–20 years, research on plant invasion patterns in mountains has increased markedly. However, published studies are unevenly spread across mountains worldwide. While there are many studies from regions with temperate or Mediterranean climates, there are few from the subtropics and tropics (e.g., the Andes, mesoamerica, Africa, and Asia) or high latitude boreal and Arctic regions. A second shortcoming is the lack of long-term monitoring of alien species in mountains. Few studies have used permanent monitoring sites to document changes in alien species occurrence in mountains (but see Kalwij et al., 2015; Turner et al., 2021). The Mountain Invasion Research Network (MIREN, www.mountaininvasions.org) has developed a standardized survey protocol to study and monitor patterns of plant invasions into mountains (but not in Africa), which has been applied in 19 regions worldwide since 2007 (Haider et al., 2022; **Figure 2.34**). While assessing future trends of alien plant species distributions in mountains remains a challenge, efforts are being conducted to model invasions using data collected at multiple scales especially under climate change (Lembrechts et al., 2017; Petitpierre et al., 2016) and shifts in biotic interactions using evidence collected through both observational and experimental approaches. Such studies show that future plant invasions in mountains will increase in the future under climate change and increased anthropogenic pressure (Alexander et al., 2016; Petitpierre et al., 2016).

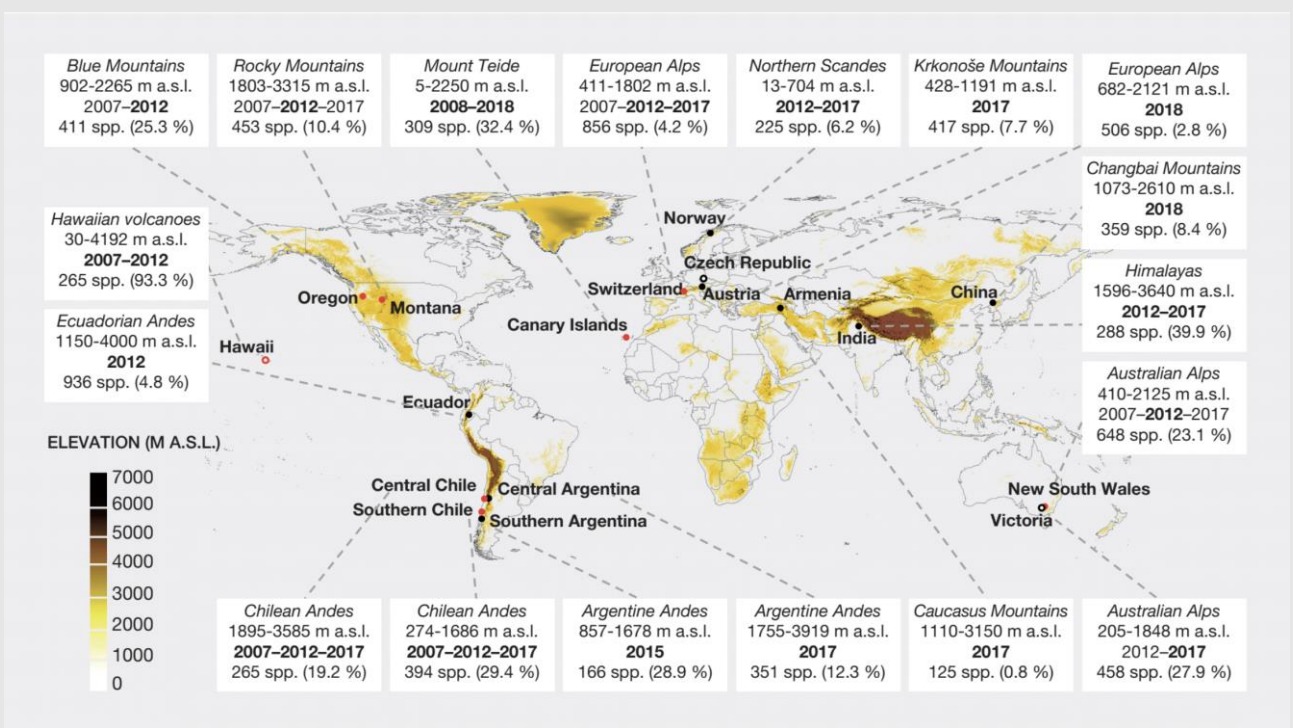

Figure 2.34. Locations of the MIREN surveys. Sites in mountain regions where MIREN surveys have been used to sample and monitor plant invasions across elevational gradients. Source: Haider et al. (2022), https://doi.org/10.1002/ece3.8590, under license CC BY 4.0.[3]

2.5.2.1. Tropical and subtropical dry and humid forests

Tropical and subtropical forests cover about 52 per cent of global forested land and hold 200 billion tons of carbon in aboveground biomass (IPBES, 2019a). These ecosystems harbour the highest biological diversity globally, but also the highest number of threatened species (IPBES, 2019a). Since 1990, over 250 million hectares were cleared for agriculture and urban expansion, infrastructure and mining (IPBES, 2019a; Vancutsem et al., 2021). Although some regions have reported net gain in forest cover, this trend is mainly driven by planted-forest expansion with alien tree and palm species (Sloan & Sayer, 2015).

Trends

Historically, tropical and subtropical dry and humid forests have experienced fewer introductions of alien species relative to temperate ecosystems. Compared to other mainland terrestrial regions of the globe, tropical and subtropical dry and humid forests have lower numbers of invasive alien species for all taxonomic groups (Dawson et al., 2017). For instance, records of invasive alien species in the tropical and dry forests of South America mostly date from the past 50 years and have increased only in the last 20 years (Zenni, 2015; Zenni & Ziller, 2011). Also, tropical South America has two or three times fewer established alien plants than temperate South America despite its greater area (Zenni et al., 2022). However, the recent and ongoing increases in biological invasions in tropical and subtropical dry and humid forests can be attributed in large part to

[3] This map is directly copied from its original source (Haider et al., 2022) and was not modified by the assessment authors. The map is copyrighted under license Attribution 4.0 International (CC BY 4.0). The designations employed and the presentation of material on the maps used in the assessment do not imply the expression of any opinion whatsoever on the part of IPBES concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. These maps have been prepared or used for the sole purpose of facilitating the assessment of the broad biogeographical areas represented therein and for purposes of representing scientific data spatially.

agricultural and urban expansion and increased propagule pressure (Waddell et al., 2020). Forest degradation and clearcutting allow the establishment and spread of numerous invasive alien grass species, some of the most prominent invaders in tropical forest ecosystems (Dar et al., 2019; Zenni, 2015; Zenni & Ziller, 2011).

Lack of reliable baseline information from most countries in Asia prevents a comprehensive analysis of trends of alien plant invasions in tropical and subtropical forests in this region. Available information shows an increase of one to eight major species during a period of 7-18 years in five countries in the region (Banerjee et al., 2021; Government of Myanmar, 2005; Islam et al., 2003; Khuroo et al., 2012; Mukul et al., 2020; Pallewatta et al., 2003; Shrestha & Shrestha, 2021; Tiwari et al., 2005; Wijesundara, 2010).

Status

Some tropical and subtropical dry and humid forests on islands have some of the most noteworthy examples of biological invasions. Hawaii, for instance, has a greater number of established alien species than native species (G. W. Cox, 1999). Species such as *Psidium cattleianum* (strawberry guava), *Morella faya* (firetree), *Hedychium* spp. (ginger), and *Sus scrofa* (feral pig) have caused significant ecological impacts in Hawaiian tropical forests. Another highly invaded tropical island, the Galapagos, considers biological invasions the most relevant threat to native biodiversity and the alien taxa outnumber the native species (Zenni et al., 2022). In Guam, invasive alien reptiles (notably *Boiga irregularis* (brown tree snake)) and some invasive alien tree species have been reported to extirpate native species and drastically change ecosystem processes (Fritts & Leasman-Tanner, 2001; Marler, 2020).

In South America, there are 247 known established alien plant species in Bolivia, 503 in Brazil, 265 in Colombia, 348 in Ecuador, 166 in Guyana, 72 in Paraguay, 288 in Peru, and 219 in Venezuela (Zenni et al., 2022). For the Caribbean, there are at least 446 invasive alien species known among plants, invertebrates, vertebrates, fungi, and diseases (Kairo et al., 2003). *Herpestes javanicus auropunctatus* (small Indian mongoose) is one of the most notorious of these species in the Caribbean as it has been associated with the extinction of five native species. In Asia, 179 invasive alien species have been recorded in tropical forests of central India (Dar et al., 2019). For plants, the numbers of invasive alien plants in tropical and subtropical forests (based on data from 10 countries) range from 15 to 58, the highest being in forests of Indonesia (58 species) followed by forests in China (52) (Banerjee et al., 2021; Mukaromah & Imron, 2019; Mukul et al., 2020; Qureshi et al., 2014; Shrestha & Shrestha, 2021; D. T. Tan et al., 2012; Weber et al., 2008; Wijesundara, 2010; H. Xu et al., 2012). The most widespread species in the region are *Lantana camara* (lantana) (recorded in 18 countries of the 19 for which data are available), *Leucaena leucocephala* (leucaena, 18 countries), *Mikania micrantha* (bitter vine, 16 countries), *Ageratum conyzoides* (billy goat weed, 16 countries), *Chromolaena odorata* (Siam weed, 15 countries), *Mimosa diplotricha* (giant sensitive plant, 13 countries), *Prosopis juliflora* (mesquite, 12 countries) and *Parthenium hysterophorus* (parthenium weed, 11 countries).[4] In India, the invasive alien plant *Chromolaena odorata* dominates the understory of forests and has been shown to negatively affect the pollination of native species (Peh, 2010; **Chapter 4**, **section 4.4.3**). Another invasive alien plant *Lantana camara*, a plant species native to South America and invasive in most tropical regions of the world, can greatly reduce the productivity of economically important plants (Peh, 2010).

In Africa in recent decades the establishment of alien tree plantations, mainly pines and eucalyptus, has been a high priority in governmental forestry (Obua et al., 2010; Tumushabe & Mugyenyi, 2017). The replacement of natural forests with alien species, coupled with other human

[4] Data extracted from the Global Invasive Species Database (GISD; http://www.iucngisd.org/gisd/), GRIIS (https://doi.org/10.5281/zenodo.6348164) and Association of South-east Asian Nations (ASEAN; https://asean.org/)

disturbances, has compounded the threat of invasive alien species that include plants such as *Broussonetia papyrifera* (paper mulberry), *Senna spectabilis* (whitebark senna), *Lantana camara* (lantana; Totland et al., 2005), and also insect species like *Gonometa podocarpi* (podocarpus moth; FAO, 2012), *Achaea catocaloides* (African apple tree moth; e.g., Martins et al., 2015) and *Leptocybe invasa* (blue gum chalcid; FAO, 2012). These invasive alien species have the potential to pose a threat to forest ecosystems (Hamilton et al., 2016). However, very little is known about the invasion of alien species into tropical forests and there is no up-to-date detailed assessment of the potential risks that these invasive alien species, especially under rapidly changing climate, are causing to the forests and their associated biodiversity and nature's contributions to people (**Chapter 3**, **section 3.3.4**).

Data and knowledge gaps

A worldwide review of invasive alien species in tropical and subtropical dry and humid forests has never been done, and most data available to date are at the country-level rather than at the level of biogeographic regions such as units of analysis. Of the countries with major areas covered by tropical and subtropical dry and humid forests, data are available mostly for South America, some parts of Mesoamerica and the Caribbean, and for South Asia, while data is scarce for tropical and subtropical dry and humid forests in Africa.

Biological invasions in tropical and subtropical dry and humid forests have been less studied than most other terrestrial ecosystems. This lack of data is, in part, explained by the lower numbers of invasive alien species recorded for tropical forests compared to other ecosystems. However, given the growing anthropogenic pressure over these regions, it is likely that biological invasions will increase in the next decades in tropical and subtropical forests, especially in regions with high intensity of land use change. Most reports available for tropical and subtropical dry and humid forests are for plant invasions, and there is very limited data on animal invasions except for a few well-studied species, such as *Herpestes javanicus auropunctatus* (small Indian mongoose) and *Boiga irregularis* (brown tree snake). For most regions with these forests, lists of established plant species are available (Pyšek, Pergl, et al., 2017; van Kleunen et al., 2019), but these data provide very little insight into the actual situation of biological invasions in tropical and subtropical dry and humid forests (e.g., spread and impacts).

As a general trend in Asia, the cumulative number of invasive plants is known to increase exponentially over years (e.g., in China: H. Xu et al., 2012). However, information on trends and status of invasive alien plants in tropical and subtropical forests in Asia are largely unavailable. Attempts are currently being made by some countries to prepare national inventories for invasive alien plants (e.g., Dorjee et al., 2020; Mukul et al., 2020), though these lists do not appear to include information on the habitats in which the alien species occur.

2.5.2.2. Temperate and boreal forests and woodlands

Trends

The view that forested ecosystems are resistant to invasions by alien plants has eroded over the past two decades as observations of local dominance by both herbaceous and woody invaders in forests worldwide accumulate (Fridley, 2013; Liebhold et al., 2017; P. H. Martin et al., 2009). Although estimates of trends in alien plant richness specific to forests are difficult to determine for most regions, biological invasions in temperate forests are increasing globally and will likely accelerate as high latitudes continue to warm with climate change (Pauchard et al., 2016; **Chapter 3**, **section 3.3.4**), particularly for boreal forests (Mulder & Spellman, 2019; Sanderson et al., 2012). Habitat fragmentation and road-building activities are also principal drivers that facilitated he increase in forest plant invasions (**Chapter 3**, **section 3.3.1.2**), both as a means to disperse alien propagules

and to increase light and nutrient availability, which facilitate the growth of invader source populations that may spread into adjacent closed-canopy forests (R. O. Bustamante & Simonetti, 2005; Flory & Clay, 2009; Kuhman et al., 2010). Afforestation (i.e., plantation of trees in areas without previous tree cover) represents another driver that promotes biological invasions (Ramprasad et al., 2020). Forest invasion research lags behind that of grasslands and wetlands (Nunez-Mir et al., 2017), and temperate and especially boreal forests tend to be remote, making the early stages of biological invasions difficult to monitor (Liebhold et al., 2017). As a result, the colonization of temperate and boreal forests by alien plants is likely much greater than currently reflected in the literature (P. H. Martin et al., 2009).

Status

In the Northern Hemisphere, North American deciduous forests have a larger number of alien plant species than those of Europe and Asia (Fridley, 2013; Heberling et al., 2017), including a substantial number of alien shrubs, lianas, and small trees introduced as ornamentals (Fridley, 2008). In contrast, the most negatively impactful alien plants in European temperate forests are trees (**Chapter 4**, **section 4.3.2.1**; Campagnaro et al., 2018; Essl et al., 2011; Langmaier & Lapin, 2020), many of which were intentionally introduced for timber production or forest reclamation (e.g., *Prunus serotina* (black cherry; Closset-Kopp et al., 2007), *Quercus rubra* (northern red oak; Major et al., 2013), *Robinia pseudoacacia* (black locust; Vítková et al., 2017)), and woody species are the most numerous species in forest understory (V. Wagner et al., 2017). Deciduous forests of East Asia, which tend to have higher levels of native species richness than other temperate forests (Qian & Ricklefs, 2000), remain relatively uninvaded (B. Auld et al., 2003; Fridley, 2013; but see Wavrek et al., 2017); further, woody species in general are strongly under-represented in the alien floras of China (Axmacher & Sang, 2013; Weber et al., 2008), Korea (Heberling et al., 2017), Japan (B. Auld et al., 2003), and the Russian Far East (Kozhevnikov & Kozhevnikova, 2011). Boreal forests across the northern hemisphere are among the least invaded forest types outside the tropics (Leostrin & Pergl, 2021; Sanderson et al., 2012); however, climate change is widely expected to accelerate understory plant invasions (Mulder & Spellman, 2019; **Chapter 3**, **section 3.3.4**), and many fast-growing herbaceous alien species are already disrupting native tree regeneration in forest gaps (e.g., *Cirsium arvense* (creeping thistle); Humber & Hermanutz, 2011). In European (deciduous) forests, 386 alien plant species were recorded in forest understory and the most common, *Impatiens parviflora* (small balsam), was recorded in 21 per cent of sampled plots (V. Wagner et al., 2017). Plant invasions of forests of temperate South America remain understudied but there is some evidence that North American plantation conifers (e.g., *Pinus contorta* (lodgepole pine), *Pseudotsuga menziesii* (Douglas-fir)) are able to establish in native evergreen forests (Pauchard & Alaback, 2004; Peña et al., 2008; Simberloff et al., 2009), along with herbaceous species such as *Prunella vulgaris* (self-heal; Godoy et al., 2011). Plantation conifers (e.g., *Pinus radiata* (radiata pine)) are also an increasing concern in dry eucalypt forests of Australia (M. C. Williams & Wardle, 2005).

Data and knowledge gaps

Although alien plant lists are increasingly available for regions where forest invasions are understudied, including Turkey (Akbulut & Karaköse, 2018; Yazlık et al., 2018), Iran (Sohrabi et al., 2021), and Siberia (Vinogradova et al., 2018), the richness and abundance of invasive alien plants specific to temperate forested habitats remains unknown for many regions outside North America and Europe (Heberling et al., 2017). One of the key knowledge gaps is the role of shade tolerance in alien species establishment: many alien plants establish following disturbance and persist under a closed canopy, but relatively few alien plants can recruit into intact temperate and boreal forests (P. H. Martin et al., 2009; V. Wagner et al., 2021). A priority of future research is to understand the interplay of disturbance, climate change, and biological invasions (**Chapter 3**,

section 3.3.4) in altering the trajectory of native forest stands to what will likely become novel communities of mixed native and alien species (Chmura, 2020).

2.5.2.3. Mediterranean forests, woodlands and scrub

Trends

Although no comprehensive analysis of the trends of alien species for Mediterranean ecoregions (Mediterranean Basin, South Africa, North America, South America and Australia) exists, it seems likely that the number of alien species increases as observed for other regions. As with other units of analysis, increases in the number of alien species and rates of new records results not only from increased transport of species (e.g., trade, human population, spread, tourism; M. C. Jackson & Grey, 2013), but also from increasing wildfires (e.g., Keeley et al., 2005), increased sampling intensity (both in the field and for bibliographic searches) and greater awareness of invasive alien species (L. Henderson & Wilson, 2017). Some regions and taxa have recently shown a deceleration in new introductions as a result of successful invasive alien species management or national and transnational regulations (European Union, 2014; Murray & Phillips, 2012). This is the case with, for example, birds in the Iberian Peninsula (Abellan et al., 2016), plants and terrestrial vertebrates in Chile (Fuentes et al., 2020), and invasive plants in Australia (Murray & Phillips, 2012).

In South Africa, the South African Plant Invaders Atlas reports a general increase in both the numbers of alien plant species and total area occupied (L. Henderson, 2007). While the rate of spread of alien plants decreased in some cases and even contracted in a few cases as a result of classical biocontrol, overall, 172 new alien plant species emerged between 2006 and 2016 and those already established expanded their ranges (L. Henderson & Wilson, 2017). An increase in alien species numbers in the Mediterranean parts of the country, due to horticulture and floriculture, is reported; the area of fynbos in South Africa is referred to as one the most heavily invaded biomes in the country (L. Henderson, 1998; B. W. van Wilgen, 2018).

Some countries in the Mediterranean Basin (e.g., Portugal) have good records of temporal trends of plant species dating back to 1500. A steady increase in alien species numbers occurred over time with an acceleration in the introduction of new species at late nineteenth century, some deceleration between 1930–1940 and a new acceleration at least up to 2018 (Almeida, 2018; Almeida & Freitas, 2001). Other countries in the Mediterranean Basin, such as Albania (Barina et al., 2014), experienced accelerated introductions later during the mid-twentieth century with few alien species reported before that time.

From 1500 to 1903 more populations of alien birds were introduced to the Mediterranean parts of South Africa, Australia, California, and fewer to Chile and the north-western countries of the Mediterranean Basin. By the end of the twentieth century, this trend exhibited some changes with more bird populations introduced in the north-western countries of the Mediterranean Basin (with a hotspot in Spain), in Western Cape (South Africa) and California (United States) (E. E. Dyer, Cassey, et al., 2017). At least in the Iberian Peninsula, the pronounced increase after 1955 – particularly steep after the 1980s – was followed by a decrease by 2005, possibly explained by the ban of wild-caught birds in Spain after the avian flu and regulations to reduce invasion risk (Abellan et al., 2016).

Amphibians and reptiles were reported as introduced to Mediterranean areas only after 1800, with increasing numbers of records of new established alien species after mid-1900 (Capinha et al., 2017).

In California, United States, alien terrestrial macroinvertebrates have been established since 1700, with many species (ca. 39 per cent) introduced before 1930. A more detailed analysis from 1935 –

2010 demonstrates the regular detection of new species of alien arthropods across the 75 years in three distinct phases: higher mean values early in this period, decreased detections 1970 to late 1980s, followed by an increase (Dowell et al., 2016).

Status

Comprehensive information about terrestrial alien vascular plants is available for most countries with a Mediterranean climate (e.g., Almeida, 2018; Arianoutsou et al., 2010; Barina et al., 2014; Fuentes et al., 2020; Galasso et al., 2018; Meddour et al., 2020; B. W. van Wilgen, 2018), and most of the checklists provide information about the status of the species (Pyšek, Pergl, et al., 2017 for summary data on established alien plants).

All the Mediterranean regions share a higher percentage of alien plant species with southwest Australia than with any other region. Chile and the Mediterranean Basin share comparatively fewer alien plant species with the other regions (Arianoutsou et al., 2013). Common invasive plants in and from Mediterranean areas are *Oxalis pes-caprae* (Bermuda buttercup), *Acacia* spp., *Carpobrotus edulis* (hottentot fig), *Ulex* spp. (Gorse), *Cytisus* spp., and *Hakea* spp. (Pincushion tree). Most Mediterranean areas also share alien species that have originated from different climates, e.g., *Ailanthus altissima* (tree-of-heaven), *Conyza* spp., and *Agave americana* (century plant).

Publications on alien plants are more common than for other taxonomic groups (e.g., Chile; Fuentes et al., 2020; N. J. van Wilgen et al., 2018; IUCN SSC Invasive Species Specialist Group (ISSG)). In Mediterranean areas, alien bird species richness is high in some regions of California, western parts of the Mediterranean basin, South Africa, and Australia (E. E. Dyer, Cassey, et al., 2017). Alien reptiles and amphibians (Capinha et al., 2017) present in the five global Mediterranean areas are more numerous in terms of species numbers in California and Spain, and have few documented species (or are even absent) in northern Africa and Eastern Europe. Terrestrial invertebrates also show high numbers of alien species, for example, in California (over 1,600 species, approximately 85 per cent insects) (Dowell et al., 2016).

Data and knowledge gaps

In countries covering multiple units of analysis, the trends and status for alien species in the Mediterranean zone is mostly not specifically described. Some countries with Mediterranean climates, particularly Syria, Lebanon, Malta, and Macedonia, have not yet published comprehensive inventories of alien species. Detailed distribution maps of specific alien species in Mediterranean areas are not frequently found.

2.5.2.4. Arctic and mountain tundra

Trends

Early introductions of alien plant and vertebrate species in polar regions were largely intentional (e.g., revegetation of industrial sites and fur farming (Forbes & Jefferies, 1999; Usher, 2005), while current introductions are often unintentional (Tolvanen & Kangas, 2016; Wasowicz et al., 2020). Future increases in alien species richness across taxonomic groups for both Arctic and mountain tundra regions is expected due to climate change and increasing anthropogenic activity including deliberate ornamental plant introduction related to tourism development or unintentional introductions along roads, trails, and mineral extraction sites (**Chapter 3**, Carboni et al., 2018; Nielsen & Wall, 2013; Normand et al., 2013; Petitpierre et al., 2016; Solovjova, 2019; C.-J. Wang et al., 2017; Ware et al., 2016; Wasowicz et al., 2013). However, a modelling study on the 100 world's worst invaders projected no increase in suitability of tundra regions to invasive alien species until 2100 as climatic conditions for some of these species might become too extreme in the

future, or as ongoing degradation and land use change might render current habitats unsuitable (Bellard, Thuiller, et al., 2013). Invasive alien disease risks are likely to increase in the future under climate change, with potential increases in disease transmission between domestic species and Arctic wildlife, as well as through increased survival probability and range expansion of introduced disease vectors or increased host susceptibility under climate change (Bradley et al., 2005; Dudley et al., 2015; Kutz et al., 2004; Waits et al., 2018).

Similarly, mountain regions have been mostly spared from biological invasions because of low anthropogenic pressure and harsh climates (Kueffer et al., 2013; Pauchard et al., 2009; Petitpierre et al., 2016). However, many high mountain regions globally have increasing alien species richness, especially for plants (Alexander et al., 2016; Becker et al., 2005; Carboni et al., 2018; Pauchard et al., 2009; Pickering et al., 2007; Williamson & Fitter, 1996). Future alien species colonizers are expected to have wide climatic niches (like most current invasive alien species) and will likely increase their range sizes from low elevations via an upward expansion of their current range limits, with expansion rates for alien plants being twice as high as for native plant species (Alexander et al., 2011, 2016; Carboni et al., 2018; Dainese et al., 2017). Direct introductions of more specialized (i.e., cold adapted) alien species into high elevation environments will also likely increase because of increased tourism and targeted introduction for ornamental purposes (Alexander et al., 2016; Carboni et al., 2018; Godde et al., 2000; Kueffer et al., 2013; McDougall et al., 2005). Genetic adaptability of alien species at range margins resulting in the colonization of cooler sites will likely further increase the risk of future invasions (Alexander, 2010). Bryophytes are common alien species in cold environments (Rozzi et al., 2008) and the likelihood of alien bryophytes invading high mountain and Arctic tundra ecosystems is assumed to be high (Essl et al., 2013; Pauchard et al., 2016).

Status

Established alien species richness across taxonomic groups decreases towards higher latitudes (Capinha et al., 2017; E. E. Dyer, Cassey, et al., 2017; Essl et al., 2013; Pyšek & Richardson, 2006; Qian, 2008; Sax, 2001) and high elevations (M. Ahmad et al., 2018; Alexander et al., 2011; Q. Guo et al., 2021; Haider et al., 2010; Kalwij et al., 2008; Khuroo et al., 2011; Marini et al., 2013; Western & Juvik, 1983), but exceptions exist (Paiaro et al., 2011; Rosa, 2020). Arctic regions have been identified as coldspots for alien species richness across different taxonomic groups (e.g., plants, birds, mammals, spiders, ants, amphibians, reptiles, fishes), especially Greenland, northern North America and northern Europe (Dawson et al., 2017). Alaska and northern Central Asia have higher alien richness of several taxonomic groups, but these patterns might be influenced by different sampling intensity and data availability across regions (Dawson et al., 2017). In mountain and arctic tundra, alien plants are generally found in anthropogenically disturbed sites and along transportation infrastructure routes (Alexander et al., 2011, 2016; Forbes & Jefferies, 1999; Haider et al., 2010; Kalwij et al., 2008; Khuroo et al., 2011), and their richness decreases with increasing distance from these structures (Arteaga et al., 2009; Haider et al., 2022; Pauchard & Alaback, 2004; Seipel et al., 2012). Successful invaders are mainly graminoid or weedy species (Alexander et al., 2016; Carey et al., 2016; Forbes & Jefferies, 1999; Wasowicz et al., 2020) however, primary invasion along mountain roads tends to promote longer lived species (McDougall et al., 2018). Species richness increases across taxonomic groups are mainly linked to invasions from lower elevations and latitudes under climate change, and increasing anthropogenic pressure associated with intentional introductions (Alexander, 2010; Bertelsmeier et al., 2015; Carboni et al., 2018; Dainese et al., 2017; Godde et al., 2000; Greve et al., 2017; Kueffer et al., 2013; McDougall et al., 2005; Parkinson & Butler, 2005; Wasowicz et al., 2013, 2020) but some invasive alien species might also lose suitable habitats when the climatic conditions become too extreme in the future (Bellard, Thuiller, et al., 2013).

Data and knowledge gaps

No dedicated gap analysis is currently available for Arctic and mountain tundra regions. However, the same regional gaps emerge across taxonomic groups as for global alien richness datasets. In particular, data is missing for most taxonomic groups in the northern part of Asia (Dawson et al., 2017) and research efforts are generally less intensive for animals and plants at higher latitudes (Lenoir & Svenning, 2015). Given that animals and plants are two of the most studied taxonomic groups, this is likely also true for other taxonomic groups such as mosses, lichens, and microorganisms.

2.5.2.5. Tropical and subtropical grasslands

In the Millennium Ecosystem Assessment (2005) tropical grasslands and savannas were regarded as less affected by plant invasions relative to other biomes, but there is an increasing trend in both distribution and alien species richness in these biomes. Thus, although invasive alien species have only recently been considered as a main threat to biodiversity conservation and functioning of tropical grasslands and savannas, they are likely to become much more widespread in the future. Within the grassland-savanna biome, frequently seasonally flooded river and stream banks are generally substantially more vulnerable to plant invasions than areas away from rivers (Pyšek, Hulme, et al., 2020; D. M. Richardson et al., 2007), but with notable exceptions.

The current low incidence and impact of alien plants in savannas relative to some other terrestrial biomes may be because disturbance, which generally favours invasions, is fundamental to savanna functioning (**Chapter 4**, **section 4.3.2.1**). Savannas are resilient to changes in disturbance regimes (Harrison & Shackleton, 1999; Walker & Noy-Meir, 1982), making them relatively resistant to biological invasions in some areas (Foxcroft, Richardson, et al., 2010). Drivers facilitating plant invasions in savannas include herbivore presence, residence time, intentional introductions for pasture improvements, the introduced species' physiology, and anthropogenic disturbance (Foxcroft, Richardson, et al., 2010). While fire regimes may play a role in preventing alien plant invasions in fire prone systems, the increasing invasion of cacti (less affected by fire in areas denuded of grass cover) in African savannas, and fire adapted African grasses in northern Australian and southern American savanna grasslands are overcoming this barrier.

Trends

Although no study about trends of alien species in tropical and sub-tropical grasslands yet exists, it seems likely that the number of alien species are increasing likewise to other regions worldwide such as temperate grasslands (**section 2.5.2.6**).

Status

Foxcroft, Richardson, et al. (2010) suggested that African savannas are less invaded than savannas in the Neotropics and northern Australia, where alien African grasses especially have had significant impacts, due to (i) lower rates of intentional plant introductions to that continent, (ii) the role of large mammalian herbivores in African savannas, (iii) historical and biogeographical issues relating to the regions of origin of alien species, and (iv) the adaptation of African systems to fire. Moreover, many forms of anthropogenic land use over a long period (Bourlière & Hadley, 1983), together with high levels of frequent disturbances, may have resulted in alien plants being not yet very widespread or common in African savannas (Foxcroft, Richardson, et al., 2010). In Southern Africa, L. Henderson and Wells (1986) listed 583 established alien plants for tropical savannas, of which 151 were known to be particularly impactful invasive alien species, and L. Henderson (2007) reported 48 alien species for the savanna biome of South Africa alone. *Lantana camara* (lantana), *Chromolaena odorata* (Siam weed) and *Melia azedarach* (Chinaberry) were the most prominent

invasive alien species, followed by *Solanum mauritianum* (tobacco tree), *Acacia mearnsii* (black wattle), *Opuntia ficus-indica* (prickly pear), *Ricinus communis* (castor bean), *Psidium guajava* (guava), and *Jacaranda mimosifolia* (jacaranda). Examples of invasive alien species in protected areas include *Chromolaena odorata* in Hluluwe-Imfolozi (Macdonald, 1983) and *Opuntia stricta* (erect prickly pear) in Kruger National Park (Foxcroft et al., 2004). More recent evidence from East Africa suggests these trends of savannas being less invaded are reversing and biological invasions are rapidly increasing. While the Serengeti-Mara ecosystem in East Africa is relatively free of widespread and abundant invasive alien plants, with a few exceptions, Witt et al. (2017) report 51 established alien plant species, with 21 of these recorded as invasive. They consider *Parthenium hysterophorus* (parthenium weed), *Opuntia stricta*, *Tithonia diversifolia* (Mexican sunflower), *Lantana camara*, *Chromolaena odorata*, and *Prosopis juliflora* (mesquite) to pose the greatest threats. In central Kenya, Laikipia County, which comprises grasslands, savanna woodland and forest, 145 alien plant species recorded, 67 and 37 were already established or invasive, respectively (Witt et al., 2020). Widespread species in the county included *Opuntia stricta*, *Opuntia ficus-indica*, *Austrocylindropuntia subulata* (Eve's needle cactus), and other succulents (Witt et al., 2020).

"New World" neotropical savannas are locally highly invaded mostly by African C4 grasses introduced for forage quality improvement (e.g., *Hyparrhenia rufa* (jragua grass), *Urochloa eminii* (signal grass), *Melinis minutiflora* (molasses grass), *Andropogon gayanus* (tambuki grass), *Panicum maximum* (Guinea grass); Rejmánek et al., 2013). In Brazil, this practice was encouraged into the late 1990s (Pivello et al., 1999). In Colombia, Venezuela, and Brazil, about 4 million km^2 were transformed to pasture by using, to a large extent, African C4 grasses (D. G. Williams & Baruch, 2000). Gorgone-Barbosa et al. (2015) also reported *Urochloa brizantha* (palisadegrass) to be an aggressive invasive alien grass in the Brazilian Cerrado. Trees are, however, also invasive in grassland savanna in São Paulo State, Brazil, where De Abreu and Durigan (2011) reported that *Pinus elliottii* (slash pine) has completely altered the structure of grassland savannas.

African and European grasses are common alien species in Australia (D'Antonio & Vitousek, 1992). Lonsdale (1994) reported that 466 alien pasture species were intentionally introduced into the savannas of northern Australian and many have become invasive (ca.13 per cent). The most impactful invasive alien species in Australian tropical savannas include *Andropogon gayanus* (Tambuki grass) introduced as a pasture grass in the 1930s, whose invasion has led to several-fold increases in the fuel load and fire intensity, further promoting this species' invasion (Rossiter et al., 2003). In Kakadu, *Mimosa pigra* (giant sensitive plant), *Hymenachne amplexicaulis* (hymenachne), *Urochloa mutica* (para grass) (Setterfield et al., 2013), *Cenchrus ciliaris* (buffel grass), *Cenchrus polystachios* (mission grass), *Themeda quadrivalvis* (grader grass) are other fire-regime altering African grasses, while *Vachellia nilotica* (gum arabic tree) from Africa, *Cryptostegia grandiflora* (rubber vine) from Madagascar, *Jatropha gossypiifolia* (bellyache bush) from Mesoamerica, *Lantana camara* (lantana) from the Neotropics, *Mimosa pigra* from South America, or *Prosopis* species (mesquite) from Americas, and *Ziziphus mauritiana* (jujube) from India are examples of woody species invading Australian savannas. There are also several cactus species introduced from Meso- and South America (Foxcroft, Richardson, et al., 2010). Ratnam et al. (2019) also shows that across large stretches of fine- and broad-leaved savannas in Asia, *Lantana camara* and *Prosopis juliflora* are widespread, expanding widely over the past three to four decades.

Data and knowledge gaps

Tropical and subtropical savannas and grasslands are in regions understudied compared to other regions of the world making information about alien species scarce and comprehensive studies lacking. It therefore remains unclear to what degree the often-low numbers of reported established alien species in these ecosystems represent low research effort or true numbers. However, given the low numbers of available studies, it seems likely that numbers of established alien species are likely to be considerably higher than reported.

2.5.2.6. Temperate grasslands

Temperate grasslands once covered 5–10 per cent of the terrestrial surface (Dixon et al., 2014; White et al., 2000), yet now rank among the most threatened biomes globally due to land conversion and degradation (Hoekstra et al., 2004; IPBES, 2019a). In North America, ca. 70 per cent of the Great Plains prairie have been converted to cropland and to a lesser degree to pastures and human settlements. Intensive grazing and agricultural usage have transformed many Pampas areas of South America. Conversion is also pronounced in some parts of Central Asia (including Kazakhstan, Kyrgyzstan, Russia, Tajikistan; V. Wagner et al., 2020), but less so in highly continental Asia (Mongolia and China) where the world's largest temperate grasslands are still found (Wesche et al., 2016).

Trends

The ongoing intensifying anthropogenic pressures on grassland ecosystems including climate change will likely further accelerate the establishment of new alien species in temperate grasslands (**Chapter 3**, **section 3.3.4**; Catford & Jones, 2019).

Although comparative studies are lacking, the North American prairie appears to be the temperate grassland region most impacted by alien biota. The history of alien species introductions is linked to the arrival and spread of European settlers in the nineteenth century, and subsequent land conversion (Seastedt & Pyšek, 2011), associated with plant introductions having far-reaching consequences such as the conversion of prairies to annual grasslands dominated by Eurasian grasses such as *Bromus tectorum* (downy brome) (Mack, 1989). Intentional introductions have played a key role in this trend (Lehan et al., 2013; Mack & Erneberg, 2002). For the entire United States, the cumulative number of introduced insect, mite (Sailer, 1983), and bird (Temple, 1992) species has grown consistently since the 1800s. In Kansas, a state that falls entirely within the temperate grassland biome, the number of introduced vascular plants found outside of cultivation has been steadily increasing since the late 1800s but has slowed in the last century (Woods et al., 2005). A similar increase-and-decline pattern was reported for rangelands of Washington, Oregon, Idaho, Montana, and Wyoming (testimony of Peter Reich cited in (Mitchell, 2000) and is in line with reports for California (Rejmánek & Randall, 2004) and the United States as a whole (Seebens, Blackburn, et al., 2017).

In South American grasslands, the number of records of alien plants (C. R. Fonseca et al., 2013), invertebrates (De Francesco & Lagiglia, 2007), birds (Zufiaurre et al., 2016) and vertebrates are still increasing. However, formal trend analyses are lacking as are comprehensive reviews or summary data.

Review data on trends are missing for the Eurasian steppe biome. Although new plant species continue to colonize even highly continental Asia (Urgamal et al., 2014), they remain mainly confined to ruderal and otherwise disturbed habitats, while frequency and abundance in natural grasslands remains low. For the extensive grassland regions of Mongolia and China, an increase towards a higher share of C4 plants in the otherwise C3-dominated vegetation has been described (Wittmer et al., 2010). This is, however, attributed to a higher share of native species (*Cleistogenes* spp. and Amaranthaceae weeds) and may partly be triggered by warmer climate. In the middle of the last century, almost all introduced plants in Kazakhstan were either cultivated or confined to ruderal plants, with none recorded as colonizing temperate steppe grasslands (Pavlov, 1956). Compared to other continents, the trend in continental Asia might indicate a lower introduction pressure, harsher climate conditions, or time lag compared to temperate grasslands in other continents.

Status

The total number of organisms introduced to temperate grasslands worldwide has never been assessed thoroughly. A comparison of the proportion of alien species among all species across habitats revealed that temperate grasslands exhibit intermediate levels of invasions with lower proportions than urban or agricultural habitats but higher proportions than wetlands or planted forests (Catford & Jones, 2019). In states that lie entirely within the Great Plains of the United States (Kansas, Nebraska, North Dakota, Oklahoma, South Dakota), 790 alien vascular taxa (14.6 per cent of the flora) are found outside of cultivation, with forbs and herbs comprising the largest group (553 taxa, 70 per cent of the alien flora) (data extracted from the PLANTS Database; (USDA, NRCS, 2021). Introduced plant species have become so common in the prairies that grasslands lacking any alien species are rare (S. DeKeyser et al., 2010; Larson et al., 2001). Examples of invasive alien species include perennial C3 (e.g., *Bromus inermis* (awnless brome), *Poa angustifolia* (Kentucky bluegrass); E. S. DeKeyser et al., 2015; Otfinowski et al., 2007) and C4 (*Bothriochloa ischaemum* (yellow bluestem), *Dichanthium sericeum* (silky bluegrass); Mittelhauser et al., 2011; Simmons et al., 2007) grasses introduced as forage grasses, as well as annual grasses (e.g., *Bromus tectorum* (downy brome); Ashton et al., 2016) and biennial and perennial forbs (e.g., *Centaurea stoebe* subsp. *australis* (spotted knapweed), *Euphorbia virgata* (leafy spurge); LeJeune & Seastedt, 2001; Dunn, 1985). Although the rate of introduction appears to have slowed in North American temperate grasslands, the regional expansion and range infilling of already introduced alien species is ongoing (e.g., *Ventenata dubia* (North Africa grass); Wallace et al., 2015).

In the central Great Plains, 14 alien earthworm species occur in the wild (J. W. Reynolds, 2016). Furthermore, *Sus scrofa* (feral pig) - descendants from stock introduced from Europe - have become invasive in the southern and northern Great Plains (Brook & van Beest, 2014; Reeves et al., 2021). *Equus caballus* (horse) have escaped and colonized some areas of Australia and the Great Plains, though are highly restricted in their current range for the latter (Nimmo & Miller, 2007; Reeves et al., 2021). Although trees are scarce in the prairie, some invasive alien species, such as *Agrilus planipennis* (emerald ash borer; insect), *Adelges piceae* (balsam woolly adelgid; insect), and *Ophiostoma* species (Dutch elm disease; fungi; Reeves et al., 2021) can damage trees that grow locally.

In South America, around 350 alien plant species have been recorded for the Pampa regions, of which ca. 50 occur in natural and semi-natural grasslands (C. R. Fonseca et al., 2013). In Brazil, the Pampa region had the highest proportion of established alien species relative to total richness and compared to other natural regions (114 alien established alien species out of 1,685 species in total; Zenni, 2015). Invasive alien species are particularly common in the Pampas of Argentina, but also are abundant and problematic in other temperate grasslands of South America. Pampas are subject to invasion by alien shrubs from Eurasia (Mazía et al., 2010; Zalba & Amodeo, 2015) as well as by herbaceous alien species (Dresseno et al., 2018; Hierro et al., 2011). Similar to North America, the latter include alien species that have been introduced as pasture grasses, especially from Africa (*Eragrostis curvula* (weeping lovegrass), *Eragrostis lehmanniana* (Lehmann lovegrass), *Panicum coloratum* (klein grass; D. G. Williams & Baruch, 2000)), and herbs (Tognetti & Chaneton, 2012). Introduced alien pine species have been planted on a large scale in the high-altitudinal temperate grasslands of the Páramo and are showing signs of escape and spread (Hofstede et al., 2002; van Wesenbeeck et al., 2003).

In contrast, numbers of alien species are low in the harsh continental grassland regions of Asia. Several of the most important alien grasses in North American prairies originate from steppes and related grasslands (*Agropyron cristatum* (crested wheatgrass), *Bromus tectorum* (downy brome)), yet the continental climates of central Eurasia are less invaded. Mongolia, with its ca. 1 million km² of steppes, has less than 100 alien plant species (out of ca. 3200; Urgamal et al., 2014). None of these 100 alien plant species achieved high frequency or dominance in steppes, and the few studies

on invasive plants from northern China also refer to heavily disturbed areas, fields or sown grasslands rather than natural steppes (Guan et al., 2019; Xun et al., 2017). The same holds true for the extensive steppes of Kazakhstan and surrounding environments, while the steppes of Russia and Europe are heavily converted (Kamp et al., 2016; Smelansky & Tishkov, 2012). The remaining steppes of these regions often have altered plant community compositions, but the species are overwhelmingly native to the regions. Alien plants are typically confined to arable fields, and ruderal and disturbed areas (Sukhorukov, 2011; Vakhlamova et al., 2016).

Equus caballus (horse; Zalba & Loydi, 2014) and *Sus scrofa* (feral pig; Caruso et al., 2018) are known to occur in South American grasslands. Several alien bird species have established in Pampas such as *Myiopsitta monachus* (monk parakeet; Bucher & Aramburú, 2014) and *Sturnus vulgaris* (common starling; Zufiaurre et al., 2016). Data on invertebrates are more anecdotal, yet invasions have been documented for *Rumina decollata* (decollate snail; De Francesco & Lagiglia, 2007).

Data and knowledge gaps

Alien plant invasions in temperate grasslands in the Americas are reasonably well documented in the scientific literature. By comparison, the frequency and impact of other alien taxonomic groups, such as earthworms, remain understudied in these regions. Numbers of documented alien species from the steppes of inner Asia are low and it seems likely that records are missing due to low research intensity and that higher numbers could be expected, particularly in countries of low economic growth.

Records on alien animal species are incomplete with only limited reports available on common invasions in Asia. Widespread alien mammals, such as *Mus musculus* (house mouse), are even thought to have large parts of their native range in continental Asia (Appenborn et al., 2021). Baseline data are available for invertebrates and although far from comprehensive.

2.5.2.7. Deserts and xeric shrublands

Deserts and xeric shrublands correspond, in general, to regions with low population densities and several are located in countries with low per capita gross domestic product. Due to their harsh climate, few alien plants have been able to establish in these habitats (Kalusová et al., 2017). As such, they are expected to harbour fewer alien and invasive alien species than other biomes (Dawson et al., 2017). On the other hand, the harsh abiotic conditions sometimes motivated the introduction of alien species capable of surviving in such habitats to ameliorate human livelihood.

Trends

Comparing rates of alien plant species accumulation, accounting for area, the accumulation of alien plants appears to be slower in deserts and xeric habitats than in colder temperate and Mediterranean regions (Pyšek, Pergl, et al., 2017). Although these habitats used to be considered relatively resistant to alien plant invasion, the recent spread of alien species has been observed (Sandquist, 2014). In Chinese desert areas, the number of new invasive alien species is increasing (Eminniyaz et al., 2017) although this finding could also be explained by changing recording intensities. *Prosopis juliflora* (mesquite) was introduced to many desert regions starting in the 1850s and is now a widespread invader in all regions except Europe and Central Asia (Patnaik et al., 2017). *Cenchrus ciliaris* (buffel grass) was widely introduced in the early 1900s for forage and pasture and now invades large areas in Australia and Americas where it increases wildfire frequency and intensity (V. M. Marshall et al., 2012). *Camelus dromedarius* (dromedary camel) were introduced in the 1800s in Australia to assist transportation across deserts and later escaped and spread (Crowley, 2014).

The number and accumulation of emerging alien species worldwide is expected to continue to increase for most taxonomic groups and continents, though possibly more slowly in deserts and xeric shrubland compared to other biomes. Other studies predict that deserts will be unsuitable for invasive alien species by 2100 (Bellard, Thuiller, et al., 2013). Trade and transport in the subtropics (a zonobiome overlapping much of deserts and xeric shrublands) is expected to be the main driver facilitating biological invasions (Essl et al., 2020), although these areas have comparatively less trade and transport than other more populated regions (subtropics cover approximately 25 per cent of the terrestrial surface of the planet but only have 8 per cent of world population).

Status

Global analyses (Dawson et al., 2017; Turbelin et al., 2017) show some tendency for lower richness of established alien species in deserts and xeric shrublands than in temperate and Mediterranean biomes, but with some variation among regions. The Palearctic deserts in Central Asia and north Africa and the Sahara and Afrotropic deserts south of the Sahara in Africa and the southern fringe of the Arabian Peninsula (with some exceptions, e.g., Southern Africa) show relatively low numbers of alien and invasive alien species. The Australasian deserts, the Nearctic deserts in North America, the Neotropical deserts in South America and the Indo-Malay deserts south of the Himalayas tend to harbour higher numbers of established alien species, although generally much lower compared to Temperate and Mediterranean regions (Dawson et al., 2017; Turbelin et al., 2017).

The different taxonomic groups show some differences both in numbers of established alien species (many more plants than animals) and regionally. The number of established alien plants is generally lower in desert areas than in temperate and Mediterranean climates (e.g., 119 alien plants in the Nama karoo and 75 in the Succulent karoo, both in South Africa (B. W. van Wilgen & Wilson, 2018) and 73–83 alien plants in several parks of the North American Mojave Desert (Abella et al., 2015). In the desert region of Egypt only 17 alien species were reported (Shaltout et al., 2016). Following European settlement of Australia, numerous alien plant species were intentionally introduced for use in crops, pastures, gardens, and horticulture, and others arrived unintentionally. Many subsequently escaped into natural environments and are now considered as “weeds”. Of the 54 alien plant species of natural environments of arid and semi-arid Australia that are considered here, 27 were apparently unintentionally introduced, 20 were intentionally introduced, and 7 were probably introduced both unintentionally and intentionally. Livestock, including camels and their harness, and contaminated seed and hay were the most common vectors for unintentional introduction (Crowley, 2014; Friedel, 2020).

Established alien birds are absent or present in only low number in most desert and xeric habitats of the world, with a few exceptions in North American and Southern African deserts (B. W. van Wilgen & Wilson, 2018), possibly because there were few attempts to intentionally introduce alien birds in arid regions (E. E. Dyer, Cassey, et al., 2017). The number of established alien freshwater fishes is similar in both Australian and African deserts but tends to be higher in American and Asian deserts; their occurrences are associated with oases, as is the case of at least four alien freshwater fish species found in the largest oasis in the Mojave Desert (Ash Meadows), in North America (Scoppettone et al., 2005). The number of alien reptiles and amphibians introduced to deserts and xeric habitats is low (mostly below four) compared to other biomes. Regional comparisons indicate lower numbers for Palearctic deserts in Eurasia north of the Himalayas and in north Africa as well as for the Sahara, especially for amphibians (Capinha et al., 2017) than other deserts. In Southern African deserts, none or only one alien species has been reported (B. W. van Wilgen & Wilson, 2018). In a survey of eleven oases in the desert regions of Morocco, five alien ant species have been recorded spreading across seven oases (A. Taheri et al., 2021). Information about alien spiders is missing in many regions; in African deserts there are almost no alien spider species or they are not studied, but in Australian and American deserts, the numbers do not differ

much from other biomes (Dawson et al., 2017). For other animal groups, fungi, and microorganisms, little information was available except for the presence of *Batrachochytrium dendrobatidis* (chytrid fungus) associated with declines and extinctions of amphibians worldwide, in oasis of the Baja California Sur Desert, in Mexico (Luja et al., 2012).

Data and knowledge gaps

Deserts and xeric shrublands are less well-studied relative to other biomes (e.g., Crystal-Ornelas & Lockwood, 2020; Florencio et al., 2019). Global studies provide information on the status of alien species in the different desert and xeric shrubland regions, but information on temporal trends is often incomplete or even absent for most deserts. Most available studies focus on plants and animals (but not arthropods) and there were almost no studies on fungi and microorganisms (Pyšek, Hulme, et al., 2020). There is more information for the deserts of North America, but for other less well-surveyed regions, for example Africa (except South Africa) and Asia, information is scarce and limited to few species. The lack of information is particularly concerning because arid areas and desertification may be expected to increase in the future.

2.5.2.8. Cryosphere

Trends

The cryosphere has been less affected by alien species compared to other regions. The low number of reported alien species from the cryosphere have multiple reasons: The cryosphere is difficult to access, anthropogenic pressures have been low (Bennett et al., 2015; Chan et al., 2019; Galera et al., 2018; McGeoch et al., 2015; Ruiz & Hewitt, 2009; Vermeij & Roopnarine, 2008) and inhospitable environments (e.g., low nutrient soils, freezing temperatures, high UV levels) do not favour establishment of alien species. Although the Arctic and Antarctica differ, climate change and increased human activities (tourism and research) are enhancing introductions in both regions (**Chapter 3**, **Box 3.4**; Bartlett et al., 2020; Bender et al., 2016; Cárdenas et al., 2020; Chan et al., 2019; Chown et al., 2012; Chwedorzewska et al., 2015; Duffy et al., 2017; Frenot et al., 2005; K. A. Hughes, Cowan, et al., 2015; K. A. Hughes, Pertierra, et al., 2015; Huiskes et al., 2014; McCarthy et al., 2019; McGeoch et al., 2015; Miller & Ruiz, 2014; Ricciardi et al., 2017; Wasowicz et al., 2020). Plants (seeds, fragments and other propagules) and invertebrates (e.g., springtails) are introduced on clothing and personal equipment of tourists, ships, and aircraft personnel, as well as associated with packing materials (Chown et al., 2012; Huiskes et al., 2014), vehicles (K. A. Hughes et al., 2010), and fresh food imports (K. A. Hughes et al., 2011). In ten years of surveillance (2007-2017; **Glossary**) at the Scott Base in the Ross Sea region of continental Antarctica, 68 invertebrate species (15 alien within the broader Antarctic region) were intercepted on food (60 per cent), clothing and equipment (11 per cent), aircraft and cargo (11 per cent), and packaging material (11 per cent) (Newman et al., 2018). During 2007-2008 in Antarctica, over 20 alien lichens and fungi were intercepted in packaging, foodstuffs, and timber (Osyczka, 2010; Osyczka et al., 2012). Similarly, 1,019 seeds were found under the footwear of 259 travellers to Svalbard during summer 2008 alone (Ware et al., 2012), while the seeds of eight alien plant species were reported in the topsoil of Fildes Peninsula, King George Island (Antarctica), in areas intensively frequented by humans (Fuentes-Lillo et al., 2017).

In the Arctic marine environment, the rate of reported alien species rose sharply from the end of 1990 concomitantly with increased research efforts in the region. Biofouling on commercial ships is not considered an important pathway for marine alien species for the cryosphere due to the low rate of species survival (but see Chan et al., 2019), while biofouling on other vessel types (e.g., leisure crafts, fishing vessels, floating platforms) could become relevant in the future for the recent increase in tourism, fisheries, and oil and gas development in the Arctic (Chan et al., 2019). Species were mainly introduced by ballast water followed by natural spread from neighbouring areas where

the species were first introduced, and by aquaculture activities (e.g., *Paralithodes camtschaticus* (red king crab); Chan et al., 2019; Orlov & Ivanov, 1978). Similarly, in the Antarctic marine environment, species were likely introduced by vessels (three by hull fouling, one by ballast water), with the first recorded alien species (a bryozoan) dating back to 1960, followed in 1986 by a crab, and in 1996 by a tunicate and a hydroid; the most recent introduction (a mollusc) was recorded in 2019, although it is likely that this species has subsequently gone extinct (Cárdenas et al., 2020; McCarthy et al., 2019). It is important to note that there is no evidence that any of these species (bryozoan, crab, tunicate, hydroid) are established in the Antarctic (McCarthy et al., 2019). Terrestrial alien plants in the cryosphere consist of predominantly herbaceous species, mostly introduced inadvertently in association with soils or imported fodder for domestic animals (Chwedorzewska et al., 2015; Frenot et al., 2005; Wasowicz et al., 2020). In the Arctic, there are some records of alien neophyte plants reported at the end of the nineteenth century, but their number increased in the 1950s and 1970s with species mostly introduced by seed contamination and transport on vehicles (Wasowicz et al., 2020). In continental Antarctica, few alien plants have been introduced since the 1950s (e.g., *Poa pratensis* (smooth meadow-grass) was introduced unintentionally during tree transplantation experiments in the 1950s and was eradicated in 2015 (Pertierra et al., 2017).

A comprehensive review on alien invertebrates is missing for the Arctic, but detailed data are reported for the Svalbard archipelago (e.g., Wieczorek & Chłond, 2019), with 32 alien invertebrates recorded since 1928 with an increase after 1980s, mostly due to soil importation (Coulson, 2015). In continental Antarctica, alien invertebrates, such as the springtail *Hypogastrura viatical* (springtail), were reported from the 1940s onwards (Hack, 1949; K. A. Hughes, Pertierra, et al., 2015). In terms of alien vertebrates in the Arctic, four fishes (salmonids) were translocated from North America to Scandinavia and Russia for fisheries and aquaculture since the end of 1800 (Lento et al., 2019), some mammals were intentionally farmed (e.g., *Mustela vison* (American mink) from the 1920s), while others unintentionally arrived in the 1960s (e.g., *Microtus levis* (sibling vole) in Svalbard; Sandvik, Dolmen, et al., 2019). In the Antarctic region, alien vertebrates have been reported only for sub-Antarctic islands where they can survive (conditions in the Antarctica itself are probably too extreme unless the species can live synanthropically): some mammals (i.e., rats and mice) were unintentionally introduced since the eighteenth century, others (such as ungulates, cats, rabbits, salmonids) were intentionally introduced beginning in the 1950s (Frenot et al., 2005; Lecomte et al., 2013).

The number of alien species in the cryosphere is expected to increase in the future due to climate change and human pressure (**Chapter 3**, **sections 3.2.2** and **3.3.4**), but reported numbers are also expected to be higher due to the greater research effort, as noted by the growing number of publications on this area (Chan et al., 2019; Chwedorzewska et al., 2020; Duffy et al., 2017; K. A. Hughes & Pertierra, 2016; Ricciardi et al., 2017). A recent exercise of horizon scanning for future potentially invasive alien species in the Antarctic Peninsula underlined the main threat posed by marine invertebrates that can be unintentionally transported in ballast waters and on ship hulls (K. A. Hughes et al., 2020; McCarthy et al., 2019). The threat could be even greater considering the cruise ship volume from the Northern Hemisphere to Antarctica that may increase the probability of introducing species able to survive cold environments (Chwedorzewska et al., 2020).

Status

In the Arctic, 34 marine alien species have been reported, mostly crustaceans, seaweed, fish, and molluscs (Chan et al., 2019). Many more alien species are expected to arrive in the future, with Hudson Bay, Northern Grand Banks, Labrador, Chukchi, Eastern Bering Seas, and Barents and White Seas considered to be the most vulnerable areas (Goldsmit et al., 2020). 341 alien plants (188 established and 11 invasive) are reported, and their numbers are expected to increase due to a warmer climate (Wasowicz et al., 2020). The Svalbard archipelago is one of the most studied Arctic

areas for biodiversity and alien species: 98 alien and 5 established alien species are reported (Sandvik, Dolmen, et al., 2019), mostly coming from mainland Norway.

Most alien species cannot survive in Antarctic continental conditions, but several have been able to adapt to new territories by remaining in the vicinity of human settlements (i.e., research stations), where they can reproduce in more favourable conditions (K. A. Hughes et al., 2010; McGeoch et al., 2015). Up to now, only five marine alien invertebrate species have been found (plus one cryptogenic seaweed species) with free-living specimens but not established populations (Cárdenas et al., 2020; McCarthy et al., 2019). This low number of recorded marine alien species in Antarctica could be due to very harsh environmental conditions (harsher than the Arctic), incomplete assessment of local biodiversity, and limited sampling efforts (McCarthy et al., 2019). For terrestrial species in the continental Antarctic (sub-Antarctic islands excluded), there are 15 known alien species - *Poa annua* (smooth meadow-grass) and 14 invertebrates (7 Collembola, 4 Arachnida, 2 Insecta Diptera, 1 Annelida), most of which are found in the Antarctic Peninsula region (Baird et al., 2019; Enríquez et al., 2019; K. A. Hughes et al., 2020; K. A. Hughes, Pertierra, et al., 2015). This could be due to several factors. This Antarctic Peninsula is the area closest to another continent (South America), it is the least climatically extreme region of Antarctica (and has also experienced a rapid rise in temperatures since the 1950s due to climate change), and it has the largest concentration of human activity (due to research teams and tourism) resulting in a relatively high propagule pressure (K. A. Hughes et al., 2020). On the sub-Antarctic islands, which circle the continent, at least 108 alien plants, 72 terrestrial invertebrates, 16 vertebrates are reported (Frenot et al., 2005).

Data and knowledge gaps

Overall, the trends and status of alien species in the cryosphere could be better documented, even if the number of studies on this biome rapidly increased in the last years (Chwedorzewska et al., 2020). However, baseline biodiversity knowledge is poor and suitable taxonomic expertise is often lacking, making it difficult to identify alien species, particularly invertebrates and aquatic species (K. A. Hughes & Convey, 2012). For example, freshwater biodiversity is low in continental Antarctica, generally dominated by cyanobacteria, cyanophytes, bacteria, yeasts, rotifers, nematodes and diatoms; as yet, there are no reports of established alien species, but taxonomic specialists of freshwater and terrestrial Antarctic biota are rare (K. A. Hughes et al., 2020; K. A. Hughes & Convey, 2012).

2.5.3. Trends and status of alien and invasive alien species in freshwater units of analysis

Box 2.8. Rapid rise of alien fishes in the Amazon, the world's most biodiverse freshwater region

The Amazon region contains the world's richest native diversity of fishes (Toussaint et al., 2016). The extent to which this global centre of endemism has been invaded by alien species has been largely overlooked. A recent study involving 35 regional experts has documented 41 species and 17 families of alien fishes in the region, based on records that extend as far back as 1939 (Doria et al., 2021). Most (75 per cent) of these records were observed since the year 2000, during which time there has been a distinct increase in the accumulated number of alien species with no sign of saturation. This is in contrast to the classical view that biodiverse regions are resistant to invasion. More than half of these alien species are omnivores or carnivores, and are distributed for use in aquaculture or the aquarium trade. Intensive fish farming, in particular, is deemed to be a major burgeoning contributor to species introductions in the region (e.g., Doria et al., 2020).

2.5.3.1. Wetlands – peatlands, mires, bogs

Trends

Contrary to other freshwater wetlands, peatlands, mires, and bogs have generally been considered more resistant and resilient to biological invasions due to their extreme environments (such as low nutrients and oxygen, harsh climate in high mountains or salinity) and absence of anthropogenic pressure for many years (Chytrý et al., 2008; Parish et al., 2008; Zefferman et al., 2015). However, landscape transformation, due to peatland drainage for agriculture, peat extraction, deforestation, road construction, and increased international trade since the nineteenth century, is facilitating an increase of alien species in these ecosystems (Miletti et al., 2005; Parish et al., 2008; Rebelo et al., 2018; Catford et al., 2017; Pellerin & Lavoie, 2000; Tousignant et al., 2010). Indeed, many peatlands have been drained for agriculture or mined for peat, which has greatly altered their plant communities. For example, 98 per cent of the fens of the state of Ohio, United States, have been destroyed, and invasion by alien species is an ongoing concern in many remaining fens (Andreas, 1989). In Asia, increased numbers of aquatic invasive alien plants are low (0-5 species) in five countries in the region during a period of 7-18 years (Banerjee et al., 2021; Government of Myanmar, 2005; Islam et al., 2003; Khuroo et al., 2012; Mukul et al., 2020; Pallewatta et al., 2003; Shrestha & Shrestha, 2021; D. T. Tan et al., 2012; Tiwari et al., 2005; Wijesundara, 2010). A lack of baseline data from most countries impedes comprehensive analysis. Increasing anthropogenic threats posed to non-permanent wetlands, including climate change, will likely accelerate the establishment of new alien species (Catford et al., 2013).

Status

Some studies confirm the lower vulnerability of peatlands to biological invasions, with few or even no alien species reported for these areas (Chytrý et al., 2008; Lambdon et al., 2008; Rejmánek et al., 2013; Zedler & Kercher, 2004). For example, in Europe almost 10 per cent of all alien plants occur in peatlands (Lambdon et al., 2008) with frequency of plants introduced after 1500 spanning from 0 in Catalonia and Czech Republic to 0.2 per cent in the United Kingdom (Chytrý et al., 2008). An assessment of Natura 2000 areas in Poland (Perzanowska et al., 2019) showed that the majority of bogs, mires, and fens host a low number of alien species (maximum 10 species), occurring at low frequency. Other studies underline the increasing effect of the anthropogenic pressures on peatlands and the subsequent higher occurrence of alien species (e.g., Jukonienė et al., 2015).

In contrast to peatlands and bogs, riparian habitats are among the most invaded habitats (Catford & Kyle, 2016; Vilà et al., 2007). A study comparing numbers of established species in European habitats (Pyšek, Bacher, et al., 2010) showed that riparian and aquatic habitats are most heavily colonized by alien mammals and herptiles; the latter group is also reaching high species densities in mires. The highest densities of alien bird species are found in aquatic and cultivated habitats. Overall, riparian habitats appear highly invaded by all groups of animal taxa except insects. For plants, alien species numbers from riparian habitats were almost as high as for urban habitats (Pyšek, Bacher, et al., 2010).

Across Asia, the number of invasive alien plants in non-permanent freshwater ecosystems range from 5-13 species in 13 countries (Banerjee et al., 2021; Kurniawan & Paramita, 2020; Mukul et al., 2020; Qureshi et al., 2014; Shrestha & Shrestha, 2021; Sujanapal & Sankaran, 2016; Weber et al., 2008; Wijesundara, 2010; H. Xu et al., 2012). The most dominant species in the region are *Pontederia crassipes* (water hyacinth, recorded in 17 countries of the 19 countries for which data are available), *Pistia stratiotes* (water lettuce, 17), *Salvinia × molesta* (kariba weed, 12), *Mimosa*

pigra (giant sensitive plant, 11), and *Alternanthera philoxeroides* (alligator weed, 10).[5] Some of the new additions to the region include *Cabomba caroliniana* (Carolina fanwort) and *Typha angustifolia* (lesser bulrush). In Kolkheti Lowland (Georgia), 423 alien plants are reported, 308 of which are present in peatland areas: the introduction of these species was favoured by the increased transformation and anthropization of the areas in the nineteenth century (Parish et al., 2008). Wagner et al. (2017) found that, among the 83,396 plots of woodland habitats in Europe, broadleaved bog woodlands on acid peat have the second highest mean relative alien species richness per plot (2.2 per cent), probably due to a higher degree of human disturbance (e.g., peat extraction) and the invasiveness (**Chapter 1**, **section 1.4.3**) of some alien species like *Prunus serotina* (black cherry).

Drainage can favour the accessibility of these areas for tourists, facilitating the unintentional introductions of alien species (Parish et al., 2008): in 2018 *Drosera rotundifolia* (common sundew) was found in a peat bog in Nahuel Huapi National Park (Argentina) and its introduction seems related to tourists visiting the area (Vidal-Russell et al., 2019). Other disturbances can promote alien species introduction and spread: in the montane bogs of Haleakala National Park, Hawaii, undisturbed bogs were less invaded, while bogs with feral alien pigs showed an increase in invasive alien plants (Loope et al., 1992). A similar result was found in other areas: in a *Sphagnum*-dominated peatland in the Central Andes of Colombia, increased nutrient additions and physical disturbance due to agricultural activities led to the widespread occurrence of *Cenchrus clandestinus* (Kikuyu grass; Urbina & Benavides, 2015); in a New Zealand bog modified by the surrounding agricultural activities, a higher occurrence of alien invertebrates has been reported compared to undisturbed bogs (Watts et al., 2020). Finally, in some cases, natural and prescribed fires can favour biological invasions in these ecosystems. At Kaituna Wetland, Bay of Plenty (New Zealand), fire disturbance promoted more alien species (Christensen et al., 2019): after four years, the authors found 14 alien vascular species and 10 native species in burnt plots vs 10 alien species and 18 native species in unburnt plots. A similar situation is reported for the United Kingdom where in burnt plots the invasive alien moss *Campylopus introflexus* (heath star moss) was more abundant and present than the native cotton grass *Eriophorum vaginatum* (hare-tail cotton-grass; Noble et al., 2017).

Data and knowledge gaps

There is a lack of comprehensive and in-depth studies on alien species in peatlands across different continents and involving all taxa. The literature mostly presents scattered specific studies, focused on Europe and North America, which are biased towards plants. Information about the temporal trends of alien species in peatlands, bogs and mires, and their status are also mostly missing.

2.5.3.2. Inland surface waters and water bodies/freshwater

Trends

The number of alien species in freshwater has been reported to increase all over the world (Cowie, 1998; Hussner et al., 2010; O'Flynn et al., 2014; Ricciardi, 2001; Roll et al., 2009). The trends in rising alien species numbers are very consistent across all taxonomic groups such as aquatic invertebrates (Mangiante et al., 2018; Muñoz-Mas & García-Berthou, 2020; Rabitsch & Nehring, 2017; Roll et al., 2009), vertebrates (A. B. Kumar, 2000; Muñoz-Mas & García-Berthou, 2020) and plants (Hussner et al., 2010; Mangiante et al., 2018; Rabitsch & Nehring, 2017), across habitats such as lakes (Ricciardi, 2001) and rivers (M. C. Jackson & Grey, 2013; Rabitsch & Nehring, 2017) and across continents such as Europe (M. C. Jackson & Grey, 2013; Rabitsch & Nehring, 2017),

[5] Data extracted from the GISDP (http://www.iucngisd.org/gisd/), GRIIS (https://doi.org/10.5281/zenodo.6348164) and ASEAN (https://asean.org/)

North America (Mangiante et al., 2018; Ricciardi, 2001), and Asia (Roll et al., 2009). Comprehensive studies for Africa, Australasia, and South America (**Boxes 2.8** and **2.9**) are mostly lacking, but global studies and studies of individual taxonomic groups suggest similar increasing trends (Madzivanzira et al., 2021). In many cases, increases in freshwater alien species numbers accelerated after 1950 (Chambers et al., 1999; Hussner et al., 2010; Mangiante et al., 2018; Mills et al., 1993; Muñoz-Mas & García-Berthou, 2020; Roll et al., 2009), while other studies show consistent increases since 1900 (Rabitsch & Nehring, 2017) or even 1800 (Ricciardi, 2001). The observed acceleration may, however, also result from increased sampling intensity and greater awareness in more recent years (Belmaker et al., 2009; C. J. Costello & Solow, 2003).

Numbers of alien freshwater vertebrates seem to have been increasing for longer compared to invertebrates, although this may also be a consequence of varying sampling intensity and better taxonomic and ecological knowledge (Muñoz-Mas & García-Berthou, 2020). The number of alien insects in freshwaters is comparatively low even though aquatic insects are frequent in native faunas (Fenoglio et al., 2016; Guareschi et al., 2013; Muñoz-Mas & García-Berthou, 2020). This has been attributed to a combination of factors including low economic impact and low probability of transport and survival of alien aquatic insects (Fenoglio et al., 2016). Furthermore, not only has the number of freshwater alien species consistently increased, but the rates of new records over time also rose continuously (M. C. Jackson & Grey, 2013; Leuven et al., 2009; Muñoz-Mas & García-Berthou, 2020; Ricciardi, 2001). Declines in new records of alien species have been observed in a few studies recently (i.e., after 2005), but these declines are likely due to lags in detection and reporting of new alien species (Mangiante et al., 2018; Muñoz-Mas & García-Berthou, 2020; Seebens, Blackburn, et al., 2017). Increases in either species numbers or rates of new records have been associated with increasing import volumes (Cowie, 1998; M. C. Jackson & Grey, 2013; Ricciardi, 2001; Seebens, Essl, et al., 2017), human population size (M. C. Jackson & Grey, 2013), and tourism (Cowie, 1998). Similar increases are reported for alien plants as shown by the Joint Nature Conservation Committee River Macrophytes Database that contains records from standardized vegetation surveys of rivers from across the United Kingdom. Surveys focus on rivers with existing or potential conservation value, and almost 4500 surveys have been undertaken since 1977. River sites were surveyed both pre- and post-1990. Results showed a 31 per cent increase in the presence of invasive alien plant species across two survey periods in the United Kingdom (Pattison et al., 2017).

Status

Although probably due in large part to a knowledge bias, biological invasions in aquatic systems represent only a small fraction of all invasions; for example, of the 2,033 alien species recorded in South Africa, only 191 are aquatic; of these, most are freshwater invasive alien species (Skowno et al., 2019). Global maps of the distribution of alien species exist for fishes (Dawson et al., 2017; Leprieur et al., 2008) and amphibians (Capinha et al., 2017). In both cases, consistently high numbers of alien freshwater species have been reported for Europe and North America, including Hawaii, while hotspots of alien freshwater fishes have also been found in South-East Asia, Central Asia and mesoamerica (e.g., Dawson et al., 2017; Leprieur et al., 2008; **Boxes 2.8** and **2.9**). Leprieur et al. (2008) reported occurrences of 9,968 alien fish species in 1,055 river basins worldwide, with up to 95 per cent of present fish species being alien. The global distribution of alien freshwater fishes has been attributed to high per capita gross domestic product and high human population density (**Chapter 3**, **sections 3.2.2** and **3.2.3.6**; Dawson et al., 2017; Leprieur et al., 2008), but also high per centages of urban areas and basin areas (Leprieur et al., 2008). Many alien freshwater species have been intentionally released (A. B. Kumar, 2000; Muñoz-Mas & García-Berthou, 2020; Strayer, 2010) through, for instance, recreational fishing (Davis & Darling, 2017). Introduced fish species often represent large-bodied species (predators and herbivores) (Blanchet et al., 2010), which may alter food web structures with consequences for the whole food web (Cucherousset et al., 2012). Capinha et al. (2017) report alien populations for 78 amphibian

species, but not all might be classified as freshwater species. Significantly more alien freshwater amphibians have been found in islands compared to mainlands (Capinha et al., 2017). An important pathway for introduction is the construction of inland canals which are responsible for a large number of freshwater alien species such as invertebrates and fish (Faulkner et al., 2020; Galil et al., 2007; Katsanevakis et al., 2013; Schöll, 2007). Among alien freshwater invertebrates, most studies are available for freshwater crustaceans and molluscs (Cianfanelli et al., 2016; Cuthbert et al., 2020; Lodge et al., 2012), but no single study exists that shows the global distribution of alien freshwater invertebrates. Compared to aquatic alien animals, aquatic alien plants and algae have been under-investigated. Comprehensive reports on large-scale distributions of aquatic plants are lacking, but global assessments are available for well-investigated individual species such as *Pontederia crassipes* (water hyacinth) (Kriticos & Brunel, 2016), *Azolla filiculoides* (water fern) (Rodríguez-Merino et al., 2019) or *Lemna minuta* (least duckweed) (Ceschin et al., 2018).

Box 2.9. North American Great Lakes: An assessment of trends of alien species

The biological invasion history of a region can reveal the changing influence of transport vectors and management actions over time. The North American Great Lakes basin is the world's most invaded freshwater ecosystem (Pagnucco et al., 2015; Ricciardi, 2006). Numbers and taxonomic composition of established alien species discovered in the basin during different time periods are correlated to changes in vector and pathway activities, such as fish stocking, canal development, and transoceanic shipping (Ricciardi, 2006). Thus, the biological invasion history of the basin is punctuated by major phases distinguished by a predominance of particular taxonomic and functional groups as well as taxa from particular donor regions. During periods of fish stocking, for example, fishes and fish pathogens comprised many of the alien species discovered. Similarly, following the transition from solid ballast to ballast water in ships during the early twentieth century, alien species of phytoplankton and zooplankton were discovered more frequently (Mills et al., 1993). The opening of the St. Lawrence Seaway in 1959 marked a period in which ballast water discharge became the dominant vector of invasion. A more recent phase in the history of the basin is distinguished by a mass invasion of Ponto-Caspian species (including *Dreissena polymorpha* (zebra mussel), *Dreissena rostriformis bugensis* (quagga mussel), *Neogobius melanostomus* (round goby), *Cercopagis pengoi* (fishhook waterflea), and several others) and euryhaline invertebrate taxa with resting eggs that can survive transport in ballast tank sediments (Pagnucco et al., 2015; Ricciardi, 2006; Ricciardi & MacIsaac, 2000). Between 1959 and 2006, inclusive, the average rate of discovery of newly established alien species in the basin was 1.69 per year, or one new alien species every 7 months (**Figure 2.35**). The majority (65 per cent) of these introductions are attributable to ballast water shipping, primarily from European donor regions. However, since 2006, the overall rate of invasion has been reduced, declining by 85 per cent to its lowest level in two centuries (Ricciardi & MacIsaac, 2022) with very few invasions attributable to shipping. This abrupt shift in invasion risk follows the implementation of ballast water regulations by Canada and the United States in 2006 and 2008, respectively.

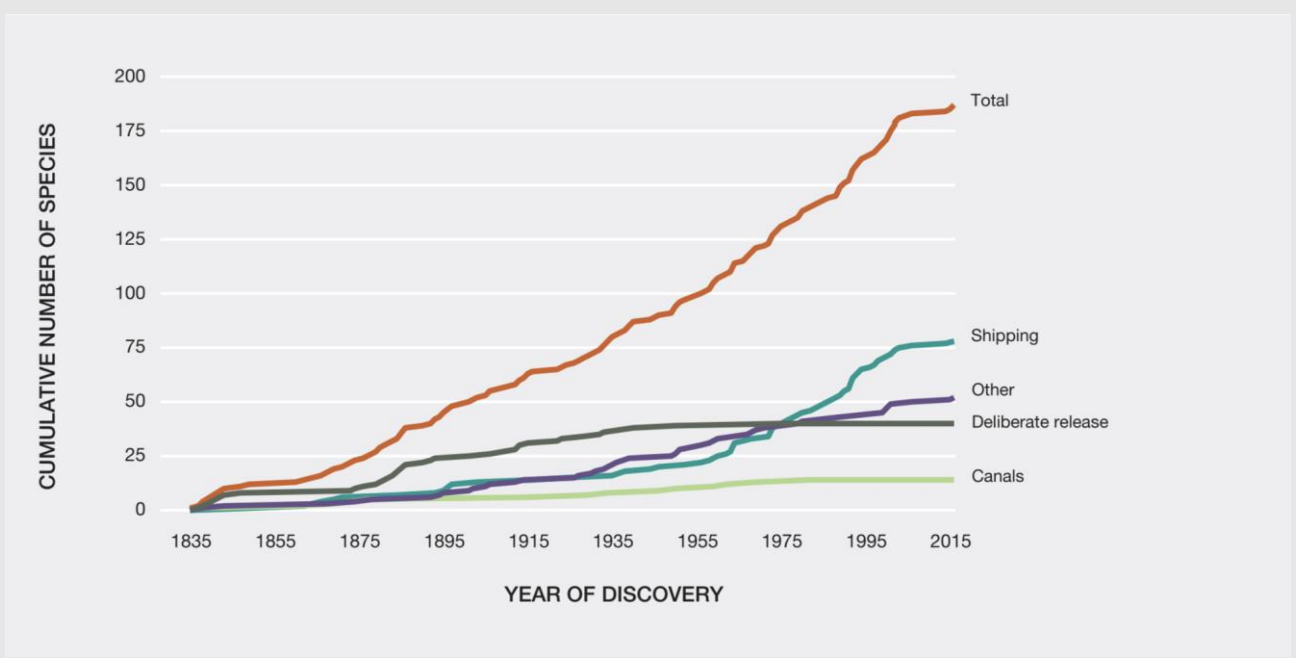

Figure 2.35. Cumulative numbers of alien species in the North American Great Lakes basin. The total number of alien species is shown in the top most line. Other trend lines show accumulations of species whose introductions are attributable to various vectors, including shipping (ballast water, solid ballast, and hull fouling), canals, deliberate release (e.g., intentional stocking of fishes), and other vectors (e.g., bait, aquarium, and unintentional releases). Data sources: Mills et al., 1993; NOAA, 2021; Ricciardi, 2006.

Data and knowledge gaps

Inland waters, riparian networks, and channels are very effective corridors for propagules that can easily be dispersed over long distances (Brundu, 2015a; Willby, 2007), but aquatic environments are difficult to monitor and an early detection of a submerged species introduction is seldom possible. No analysis reporting gaps in trends and status of alien species in freshwater systems currently exists, but a comparison of available literature reveals that freshwater systems have been far less investigated than terrestrial and (most likely) marine systems (Seebens, Blackburn, et al., 2017). Among these, the vast majority of studies have been conducted in Europe and North America, while information about the temporal trends in freshwater alien species and their status across continental ranges are largely absent. The only exceptions seem to be fishes and amphibians, for which comprehensive large-scale analyses are available (Capinha et al., 2017; Dawson et al., 2017; Kraus, 2009; Leprieur et al., 2008). However, large information gaps on species occurrences exist among these taxonomic groups, particularly in Asia and Africa (Dawson et al., 2017). Large-scale information is missing for most freshwater invertebrates, including macrophytes and algae. Riparian habitats have been extensively studied for plant invasions (Maskell et al., 2006; D. M. Richardson et al., 2007), but many studies focus on a handful of invasive alien taxa (e.g., Elderd, 2003; Hood & Naiman, 2000; Pyšek & Prach, 1993).

2.5.4. Trends and status of alien and invasive alien species in marine units of analysis

2.5.4.1. Shelf ecosystems (neritic and intertidal/littoral zone)

Trends

The number of marine alien species has been consistently and continuously increasing globally (Bailey et al., 2020) and in individual regions such as in the waters of North America (Cohen & Carlton, 1998; Ruiz, Fofonoff, et al., 2000), Europe (Gollasch, 2006; Katsanevakis et al., 2013;

Reise et al., 1998; Zenetos & Galanidi, 2020), Australia (Hewitt et al., 2004), South America (Schwindt et al., 2020; Teixeira & Creed, 2020; Toral-Granda et al., 2017), Africa (Mead et al., 2011; T. B. Robinson et al., 2020) and the Pacific (Carlton & Eldredge, 2009; Coles et al., 1999). Time series of newly reported marine alien species often date back to the early nineteenth century (Carlton et al., 2019; Carlton & Eldredge, 2009; Cohen & Carlton, 1998; Coles et al., 1999; Gollasch, 2006; Hewitt et al., 2004; Mead et al., 2011; Reise et al., 1998; Ruiz, Fofonoff, et al., 2000; Schwindt et al., 2020; Teixeira & Creed, 2020; S. L. Williams & Smith, 2007; Wolff, 2005). Likewise, increases in rates of new alien species records were frequently observed especially in the early twentieth century (Carlton & Eldredge, 2009) or after 1950 (Bailey et al., 2020; Coles et al., 1999; Gollasch, 2006; Hewitt et al., 2004; Mead et al., 2011; Ruiz, Fofonoff, et al., 2000; Schwindt et al., 2020; Teixeira & Creed, 2020; S. L. Williams & Smith, 2007). Wolff (2005) reported an increase in long-distance introduction events after 1950. Increases in marine alien species numbers are not only related to the intensifications of global shipping consistently across studies (i.e., hull fouling and ballast water), aquaculture and cultivation (including stocking and aquarium releases) (Bailey et al., 2020; Coles et al., 1999; Gollasch, 2006; Hewitt et al., 2004; Katsanevakis et al., 2013; Reise et al., 1998), but also increased tourism (Toral-Granda et al., 2017), and natural dispersal from neighbouring alien populations (Gollasch, 2006; Wolff, 2005). Rising shipping activity during both world wars is associated with new marine alien species introductions at naval bases (Coles et al., 1999). Another major pathway was the opening of new shipping canals such as the Panama Canal, the Suez Canal, and the St. Lawrence River (Galil et al., 2007; Mills et al., 1993), which resulted in large numbers of marine alien species introductions, particularly in the Mediterranean Sea (Galil et al., 2014). The extensions of these shipping canals (Galil, Boero, Fraschetti, et al., 2015; Muirhead et al., 2015), as well as the opening of new transport routes such as the Northern Sea routes through the Arctic Ocean due to climate change or the intensification of existing routes, have led to more introductions of marine alien species (Ascensão et al., 2018; Miller & Ruiz, 2014). Sudden declines in newly recorded marine alien species towards the end of the reported time series have been frequently noted (Gollasch, 2006; Wolff, 2005), which are associated with lags in detection and reporting (Wolff, 2005).

Status

One of the few global studies of marine alien species revealed hotspots in coastal areas of the North-East Atlantic, Northern European Seas, the Mediterranean Sea, Hawaiian Islands, and New Zealand (Bailey et al., 2020; **Box 2.10** for more details). Many of the reported established alien species belong to arthropods, fishes, molluscs, and algae (Bailey et al., 2020; Gollasch, 2006). The recently launched database WRiMS (M. J. Costello et al., 2021) revealed similar hotspots, although a direct comparison is difficult due to varying spatial resolutions. That said, many regions that appear to have low numbers of reported alien species (i.e., not "hotspots"), may in fact reflect more on the history and intensity of investigation rather than the intensity of invasion. Until 2019, the Galapagos Islands were reported to be invaded by only five marine species, but a re-investigation revealed a minimum of 53 marine alien species present in that Archipelago (Carlton et al., 2019). Chile is reported to have low numbers of marine alien species, with various hypotheses offered to explain the low alien species richness (Neill et al., 2020), one being low research intensity. Comparing studies of similar sampling areas such as marine bays or port regions revealed alien species numbers of similar ranges with most species found in San Francisco Bay, United States (234 species) (Cohen & Carlton, 1998) followed by the Chesapeake Bay, United States (116 species) (Ruiz et al., 1997), Port Philip Bay, Australia (99 species) (Hewitt et al., 2004), Pearl Harbor, Hawaii (69 species) (Coles et al., 1999) and Coos Bay, Oregon, United States (60) (Ruiz et al., 1997). Most of these numbers are, however, based on data that are more than 20 years old and higher alien species numbers can be expected now. For example, J. T. Carlton & Eldredge (2009) updated the Pearl Harbor number from 69 to more than 175 (many species were older invasions or of other taxonomic groups not noted in Coles et al. (1999), and thus not post-1999 invasions).

On the whole Hawaiian Archipelago, 333 marine alien species have been reported (Carlton & Eldredge, 2009, 2015). Among European Seas, by far the largest numbers of marine alien species have been recorded for the Mediterranean Sea (Galil et al., 2021b; Katsanevakis et al., 2020), followed by the North Sea and the Atlantic coast (Gollasch, 2006). Shipping (ballast water and hull fouling) and aquaculture have been consistently reported to represent the most important pathways for the introduction of marine alien species (Bailey et al., 2020; Carlton & Eldredge, 2009; Coles et al., 1999; Floerl & Inglis, 2005; Galil et al., 2014; Gollasch, 2006; Hewitt et al., 2004; Ruiz, Fofonoff, et al., 2000; Schwindt et al., 2020; Ulman et al., 2019; S. L. Williams & Smith, 2007; **Box 2.10**). Often, large numbers of marine alien species are found at sites of intense human activity such as commercial ports (Ruiz et al., 1997), marinas (Ulman et al., 2019), or disturbed habitats (Coles et al., 1999; S. L. Williams & Smith, 2007). Other vectors of introduction are fishing bait or ornamental purposes (Coles et al., 1999; Gollasch, 2006). Patterns of distribution and trends were very similar across a wide range of taxonomic groups such as macroalgae, arthropods, cnidarian, polychaeta, molluscs, and fishes (Gollasch, 2006; Ruiz, Fofonoff, et al., 2000; Seebens et al., 2016; S. L. Williams & Smith, 2007). Microorganisms were frequently introduced (Cohen & Carlton, 1998; Ruiz, Rawlings, et al., 2000); however, studies about the introduction of marine microorganisms and many other small size taxa are largely lacking.

Data and knowledge gaps

Among marine ecosystems, shelf ecosystems are much better investigated compared to the open ocean or the deep sea. Still, information about marine alien species remains one of the major gaps in the field of invasion ecology. Some high research interest regions such as North American coastlines and European Seas, including the Mediterranean Sea, are comparatively well investigated, but data is far from complete and regular monitoring does not occur (Tsiamis et al., 2021). Information for most other coastal areas is largely lacking. The most comprehensive available study on the global distribution of marine alien species shows large areas where information or expertise are lacking such as regions in Meso- and South America, Africa, and Asia (Bailey et al., 2020). Even where information is available, lists are highly incomplete for many coastal areas. Based on expert knowledge, true numbers of marine established alien species might be up to ten times higher in some regions than reported in **Figure 2.5**.

Box 2.10. Marine ecoregions: A global assessment of trends and status of alien and invasive alien species

An extensive dataset of first detection records of marine alien species from 1965–2015 across 49 marine ecoregions is provided by Bailey et al. (2020). This dataset includes three major components of alien species records including the year of first collection, the invasion status, and potential pathways of introduction. Data were analyzed at both regional and global scales to examine the patterns of first record rate, species numbers, and transport pathways.

The assembled dataset included 2,209 records of marine alien species (1,442 unique species belonged to 17 phyla) where ten ecoregions had zero confirmed records during the period of study. On a global scale, about 75 per cent of marine alien species were reported as established and about 20 per cent had unknown invasion status, while the remaining records belonged to species with failed establishments (5.4 per cent) or extinct (0.5 per cent) populations. Most of the marine alien species were likely introduced as stowaways in ships' ballast water or biofouling. Escape of species from aquaculture or mariculture followed a similar pattern, while the corridor pathway and escape of pet or aquarium species increased beginning in the late 1990s. Nearly one-third of marine alien species' records were associated with a single pathway (32.7 per cent), while most were associated with at least two (52.6 per cent), or three (14.1 per cent) pathways. However, the patterns of alien species numbers varied across regions as a result of differences in pathway strength, environmental conditions, habitat size, survey effort, and taxonomic effort. The cumulative number of records

from 1965-2015 ranged from zero to more than 500 per ecosystem, with various levels of succession of the population establishment across those regions. Ship fouling, transport stowaway, and ballast water were the dominant pathways in most regions, and were responsible for at least 40 per cent of introduction events. Other pathways became important for individual regions such as the corridor pathway (Suez Canal) in the Mediterranean Sea and escape of aquaculture/mariculture species in the East China Sea, South China Sea, and Yellow Sea (Bailey et al., 2020). Although their dataset represents an extensive global collection of marine alien species records, it only covers about 73 per cent of the world's coastal large marine ecosystems, and data coverage was low in Africa, Meso- and South America, and Asia. As discussed in Bailey et al. (2020), marine alien species have undoubtedly occurred and reported in these areas, but due to cost of marine alien species surveys, limited resources, and lack of expertise across many taxa and regions, data of sufficient quality were likely not available for their study.

2.5.4.2. Surface open ocean

Trends

Established alien species numbers are increasing in the open ocean from the tropics to polar regions due to warming oceans and human activity (M. J. Costello et al., 2021). Many marine alien species tolerate a broader thermal range than native species and are able to show rapid physiological adaptation; both characteristics give alien species more habitat opportunities than natives (Canning-Clode et al., 2011; H. Li et al., 2020). For example, "Caribbean Creep" refers to a number of marine invertebrates (e.g., *Petrolisthes armatus* (green porcelain crab)) from the Caribbean that have expanded their distribution ranges poleward and invaded the southern and mid-Atlantic United States coasts (Canning-Clode et al., 2011). Similarly, "African Creep" refers to the number of marine species moving poleward into the Mediterranean from lower latitudes (Canning-Clode & Carlton, 2017). In 1750, wooden sailing vessels could have carried 120 marine fouling and boring fauna and flora (Carlton, 1999b), while in the twentieth century, over 10,000 different marine species were estimated to be transported daily among different global geographic regions via ballast tanks (Carlton, 1999b) prior to the beginnings of detailed formulations for ballast water management. In this century, a vast global effort is underway to implement universal ballast water management strategies to prevent the transport and introduction of invasive alien species (**Chapter 5**, **section 5.5.1**).

The global rate of marine alien species records was relatively stable during 1965–1995 but increased significantly after 1995 and peaked at about 66 primary detections per year during 2005–2010, and then again decreased (Bailey et al., 2020). Arthropods, molluscs, and fishes, by far the most thoroughly studied groups, were also not surprisingly the most frequently reported aquatic alien species during this time period and were most likely introduced as stowaways in ships' ballast water or biofouling. However, direct vector-related evidence was often absent. Arctic ship-based summertime transportation and tourism also increased over the past two decades, co-occurring with sea ice reductions (IPCC, 2019). This increase might bring implications for global trade and traditional shipping corridors economies, alerting the Arctic marine ecosystems and biodiversity, such as from invasive alien species and local pollution (IPCC, 2019). The relatively recent phenomenon of floating plastic debris in the open ocean facilitates the transport of coastal and oceanic species that might normally not survive the open ocean and may result in new and more frequent introductions of alien species across the oceans (**Chapter 3**, **section 3.3.3.3**; Haram et al., 2021).

Environmental and anthropogenic changes have triggered reorganizations of reef ecology, zonation physiology, and dominance (Miranda et al., 2020). One example is the plastic pollution in the ocean such as polystyrene foam which can be a dispersal vehicle for the invasive coral *Tubastraea* spp. (sun corals) (Faria & Kitahara, 2020). For example, in Brazilian reefs *Mussismilia harttii*

(scleractinian coral) is threatened by the dominance of invasive sun corals (Faria & Kitahara, 2020; Miranda et al., 2020). Sun corals lack natural predators and can reproduce rapidly with extensive defensive mechanisms which makes them a successful invasive alien species over large areas along the Brazilian coasts (Faria & Kitahara, 2020; Miranda et al., 2020).

Status

There are more than 800 established alien species reported in the European seas only, some of which are invasive and impacting marine ecosystem services and biodiversity (Tsiamis et al., 2018, 2020). Analyses revealed that a large number of alien species were not reported in initial assessments, or were proven to be historical misreporting (Tsiamis et al., 2020). Thus, the Marine Strategy Framework Directive Descriptor 2 was implemented to provide an improved basis for reporting new alien species and to help the establishment of monitoring systems of targeted alien species (Tsiamis et al., 2020). Major intentional introductions for fisheries also occurred with deep-sea species, such as *Paralithodes camtschaticus* (red king crab), native to the north Pacific coast and released in the Barents Sea during the 1960s (ICES, 2005). The species was later captured in the Ionian Sea in the Mediterranean (Faccia et al., 2009), possibly transported by ballast water, though Faccia et al. (2009) raised doubts about whether a larva/post-larve presumably arrived in ballast water could withstand summer temperatures for so long – the specimen collected weighed about 4 kg and the estimated age was 10 years. Among tropical marine regions, Hawaii was found to be heavily affected by alien species either due to its location, governance (**Glossary**), or research effort undertaken to understand biological invasions in this region (Alidoost Salimi et al., 2021). An alternative explanation might be also due to lower native biodiversity associated with Hawaiian ecosystems providing more vacant niches being available to the alien species.

The recently launched WRiMS (marinespecies.org/introduced) is an expert-edited world list of introduced marine species and provides information of alien and invasive alien marine organisms (M. J. Costello et al., 2021). An alien marine metazoan species checklist for the Mediterranean Sea lists 573 alien species (Galil et al., 2014). Most of those alien species are thermophilic, originally from the Indo-Pacific or Indian Oceans that invaded the Mediterranean through the Suez Canal (Galil et al., 2014). Additionally, the Information System on Aquatic Non-Indigenous and cryptogenic Species (AquaNIS) database provides information on 859 aquatic alien and cryptogenic species in the North Atlantic region (AquaNIS, 2015).

Data and knowledge gaps

The open sea represents one of the least investigated units of analysis with respect to biological invasions. The size and cost of sampling the open sea presents a particular challenge. Another challenge is how "alien" is defined in the open sea because it is usually defined for much smaller geographic units such as countries - a challenging concept to transfer to the open ocean. Some databases, such as WRiMS (M. J. Costello et al., 2021), also cover the open ocean, but the vast majority of records have likely been sampled along the coasts. However, WRiMS records provide the opportunity to map the actual locations of marine alien species using records from the Ocean Biodiversity Information System (OBIS) or GBIF. Nonetheless, a comprehensive assessment of the trends and status of alien and invasive alien species in open oceans is still missing and difficult to conduct currently due to the lack of records.

There are other global databases of species occurrences such as AlgaeBase (Guiry & Guiry, 2021) or FishBase (Froese & Pauly, 2015), but the information about the status of invasion is incomplete or totally lacking. There are also distributed occurrence records for marine alien species in the GRIIS dataset (Pagad et al., 2022) and other national checklists, but these usually reflect coastal areas rather than occurrences in the open ocean. This lack of information on open ocean alien species occurrences represents one of the largest knowledge gaps across all units of analysis.

2.5.4.3. Deep sea

Trends

As biota occurring at deep ocean depths have been rarely surveyed (Saeedi, Costello, et al., 2019; Saeedi et al., 2020; Saeedi & Brandt, 2020), there are too few records over too short a time period to infer trends. The deep-sea populations of alien species may follow a "boom-and bust" pattern of abundance (Strayer et al., 2017), such as documented between 1995-2002 for *Philine auriformis* (New Zealand sea slug) in southern California, United States (Cadien & Ranasinghe, 2003), settle for long-term low-abundance stability, or, following a time lag or environmental triggering event, result in greatly increased abundance. As depth increases, less measurements are available for biological variables (M. J. Costello et al., 2018; Saeedi, Bernardino, et al., 2019), making estimations of rates of biological invasion challenging in the deep ocean.

Status

Records of biological invasions into depths greater than 200 meters are rare. The intentional introduction of the economically important North Pacific *Paralithodes camtschaticus* (red king crab) in the 1960s into the Barents Sea demonstrated that the deep ocean is not immune to invasions (Dvoretsky & Dvoretsky, 2018; Jørgensen & Nilssen, 2011). Immature individuals remain on the shallow shelf (20–50 m), adult specimens mostly inhabit deep soft-bottom areas (100–400 m), migrating into shallow waters (less than 50 m) for moulting and mating (Sundet & Hjelset, 2011). Specimens of *Pterois* spp. (lionfishes) that invaded the Western North Atlantic/Caribbean region were reported from Bermuda, Curaçao, and Honduras at depths between 250 and 300m (Andradi-Brown, 2019). *Philine auriformis* (New Zealand sea slug) was introduced to the West Coast of North America (southern California, Untied States of America, to British Columbia, Canada) and occurs from the intertidal to more than 300 m (Cadien & Ranasinghe, 2003). In the south-east Mediterranean Sea, four carnivorous Red Sea species, *Champsodon nudivittis* (crocodile toothfish), *Etrumeus golanii* (Golani's round herring), *Trypauchen vagina* (burrowing goby), and *Charybdis longicollis* (lesser swimming crab) were recently recorded at depths over 200 m (Galil et al., 2019; Innocenti et al., 2017). One possible pathway of deep-sea species translocations may be deep submergence vehicles whose use has increased since the 1960s (Voight et al., 2012). It seems realistic to suggest that understanding the scale of deep-sea invasions by alien species remains one of the most important overlooked aspects of marine invasion science.

The deep sea is now also warming, as has been observed in shallow waters, and the temperature of water below 2000 m has increased since 1992, especially in the Southern Ocean (IPCC, 2019). For example, deep Mediterranean waters have warmed by 0.12 °C since the mid-twentieth century and the deep oceans now store 16–89 per cent more heat than before (McClain et al., 2012). Temperature changes and the redistribution of total energy will ultimately impact deep-sea faunal distributions and invasion rates. For example, some deep-sea fish families of Actinopterygii were identified with depths over 1000m and were proposed as invasive alien species where most of their constituent species live in shallower than 1000m (Priede & Froese, 2013). Also, the invasion of Erythrean species of the Levantine basin into the lower continental shelf and upper slope suggests biological invasions in the deep sea warrant more attention (Galil et al., 2019). The west Antarctic Peninsula shelf is rapidly warming and is expected to soon be invaded by lithodid crabs from the Ross Sea waters that have crossed the Antarctic shelf (C. R. Smith et al., 2012).

Data and knowledge gaps

Estimating the gaps in alien species distributions of the deep-sea fauna is challenging because the deep sea is the most unexplored place on Earth and there is much yet to be learned. However, alien species pose a threat to the unique, diverse, and fragile mesophotic "animal forests". Large data and

knowledge gaps therefore remain for trends and status of invasive alien species in the deep sea as well as a lack of information the actual data gaps.

2.5.5. Trends and status of alien and invasive alien species in anthropized areas

2.5.5.1. Urban/semi-urban

Urban habitats include constructed, industrial, and other artificial land, human settlements, buildings, industrial developments, transport networks and waste dump sites, but also a diversity of semi-natural and constructed green spaces. Cities contain high densities of people and are hubs of human-mediated movement of commodities. Transport linkages (e.g., airports and harbours) facilitate the introduction and dissemination of alien species through introduction pathways such as trade, tourism, and horticulture (**Chapter 3**, **section 3.2.3**; Dehnen-Schmutz et al., 2007). The intensive study of alien plants in urban areas began in a few cities around the world in the 1980s (Esler, 1987; Kowarik, 1990; Stalter et al., 1992), largely out of natural history interest. Large-scale comparisons of alien plant taxa among cities grew out of a more macroecological approach in Europe in the 1990s (Kowarik, 1995a; Pyšek, 1998), which has since given way to more recent global assessments of patterns of alien species in cities (Aronson et al., 2014; Gaertner et al., 2017).

Trends

Evidence suggests that the rate and extent of biological invasions are increasing globally (Seebens, Blackburn, et al., 2017) and cities often play important roles as hubs for the spread of alien species (Chytrý et al., 2012; McLean et al., 2017). Studies on long-term dynamics of urban floras revealed a steep increase in established alien species numbers along with accelerating urbanization during the last century (Chocholoušková & Pyšek, 2003; S. Knapp et al., 2010; Tretyakova et al., 2018), with alien species occupying a median of 28 per cent (ranging from 25-50 per cent) of their respective urban floras (Aronson et al., 2014; Esler, 1987; Ricotta et al., 2009, 2012; G.-L. Zhu et al., 2019). Several studies from around the world show that more urbanized areas tend to harbour a higher relative abundance and diversity of alien species than rural and peri-urban areas (Aronson et al., 2015; Blair & Johnson, 2008; Cadotte et al., 2017; X. Chen et al., 2014; Lowry et al., 2020), and as urbanization expands, the numbers of alien taxa in urban areas will consequently increase as well.

Projected trends in plant invasions in Europe under different scenarios of future land-use change showed the second highest level for urban areas (Chytrý et al., 2012). Most alien species in cities and urban areas are intentionally introduced ornamental plants that escaped from cultivation (Čeplová et al., 2017; Dehnen-Schmutz et al., 2007; McLean et al., 2017; Padayachee et al., 2017). Studies in the Czech Republic, for example, reveal that 47 per cent of alien species now found in cities and beyond were introduced intentionally, mostly as ornamentals (Pyšek et al., 2002), and work from South Africa showed that twice as many of the most abundant alien species in urban areas were originally introduced for ornamental purposes compared to non-ornamental alien species (McLean et al., 2017). Much like agriculture, plantings of alien plants in urban settings provide suitable habitats for the establishment of alien insects; consequently, urban settings and especially street trees tend to be hotspots for insect invasions (Branco et al., 2019; Dale & Frank, 2017; Paap et al., 2017).

It is likely that a warmer climate together with urban sprawl will increase the invasion risk for cities, especially as species from different climatic regions are transported elsewhere, and especially from warm regions to temperate ones (e.g., Géron et al., 2021; Lososová et al., 2018). For Europe, Lososová et al (2018) suggest that alien species from regions with warm climates, such as those currently limited to southern Europe, are likely to increase their rate of spread and colonize the cities of Central and Western Europe. Alien insects appear to be especially benefiting from

increased urban temperatures, for example, alien mosquitos in montane cities in South America (Pedrosa et al., 2020) and alien scale insects in the United States (Meineke et al., 2013).

Status

The most comprehensive global data set on urban floras and bird faunas, based on 110 and 54 cities on all continents, respectively, revealed that the numbers of alien species differ broadly among cities with a median of 3.5 alien bird (range: 0–23) and 213 plant species (range: 38–1058), of the total species richness 112.5 (range: 24–368) for birds and 766 (range: 269–2528) for plants. Among plants, Poa annua (annual meadowgrass), Capsella bursa-pastoris (shepherd's purse), Stellaria media (common chickweed), Plantago lanceolata (ribwort plantain), and Phragmites australis (common reed) have established in the greatest numbers of cities, while among birds such species are Columba livia (pigeons), Passer domesticus (house sparrow), Sturnus vulgaris (common starling), and Hirundo rustica (barn swallow) (Aronson et al., 2014). Further, it appears that intensive land-use change, and biotic interchange have increased the similarity of urban plant assemblages globally. Cities in disparate regions of the globe thus retain regionally distinct native and alien plant assemblages (Palma et al., 2017), while invasive alien species are associated with lower beta diversity among cities (La Sorte et al., 2014).

The numbers of established alien species of plants, insects, herptiles, birds, and mammals, introduced to Europe after 1500 and occurring in habitats defined according to the European Nature Information System were analysed for 115 regional data sets (Pyšek, Bacher, et al., 2010). Cities in Europe on average harbour 70 per cent of established alien plants (ranging from 41–100 per cent in individual regions), 54 per cent (11–76 per cent) of alien insects, 38 per cent (0–100 per cent) of alien herptiles, 14 per cent (0–33 per cent) of alien birds, and 26 per cent (0–100 per cent) of alien mammals. The numbers of established alien plant and insect species found in human-made, urban, or cultivated habitats were the highest of all habitats, if controlled for habitat area in the region (Pyšek, Bacher, et al., 2010). The patterns of urban alien diversity have not been summarized beyond Central and Western Europe, but studies from elsewhere, for example, China, Russia, and Canada, also confirm that urban areas tend to contain very high numbers of alien species (Cadotte, 2021; Tretyakova et al., 2018; Z.-X. Zhu et al., 2019).

Data and knowledge gaps

Although urban ecosystems are hotspots for biological invasions, the field of invasion science has given scant attention to invasion dynamics in towns and cities (Gaertner et al., 2017) with the exception of Europe where this topic has been subject of research for decades (e.g., Kowarik, 1995b; Pyšek, 1998; Sukopp, 2002). Many facets of biological invasions require elaboration in an urban context (Cilliers et al., 2008; Padayachee et al., 2017). The role of cities as launching sites for alien species introduction and spread into natural areas and as recipients of a range of socioecological impacts highlights the need for research to address key limitations that hinder the understanding of invasion dynamics in urban settings. There have been very few urban-rural gradient studies in developing countries (Pauchard et al., 2006), or in tropical environments in general (Cusack & McCleery, 2014). So far, the relationship between levels of urbanization and abundance of alien invasive plants in tropical developing countries appears to resemble that of temperate developed countries (Lowry et al., 2020). Limitations include the dearth of metrics for defining urban–wildland/rural gradients and a shortage of insights on many aspects of urban invasions in less affluent regions (Gaertner et al., 2017). Thus, data on alien taxonomic groups other than plants within cities and ecoregions surrounding each city is needed.

2.5.5.2. Cultivated areas (including cropping, intensive livestock farming, etc.)

Many introductions and secondary spread of alien species occur in cultivated areas. Alien plant species that occur as weeds in agricultural areas can be introduced as contaminants of seeds, or spread by machinery and grazing animals, water channels, etc. In addition, the use of plant protection products may promote the development of herbicide resistant alien weeds, as in the case of Amaranthus, Solanum, etc. In addition, agricultural areas are often first sites of new introduction of novel crops, genetically modified organisms, biofuel crops, and novel genotypes of cultigens. In some parts of the world, ornamental plants are also intensively cultivated in agricultural areas (e.g., Booth et al., 2003). Cultivated plants also suffer from introduced pathogens (e.g., fungal, viral, bacterial).

Various pathways are known to facilitate the accidental introduction of insects, pathogens, and other pests (e.g., nematodes) into cultivated areas around the world. Many groups of insects colonize stored grains and international trade in grain has facilitated the global spread of these insects such that several important species are established in virtually every world region (Morimoto et al., 2019). Other important pathways by which insect pests have globally spread include international trade in fruits and vegetables and global transport of live plants, including soil and planting substrates (Kiritani & Yamamura, 2003; Liebhold et al., 2012). Prior to 1910, there was little recognition of the dangers that such international trade posed for introduction of agricultural pests, but in the early 1900s many countries began to implement regulations aimed at limiting the accidental spread of plant pests with plants and plant parts. A variety of phytosanitary measures have been developed to limit pest movement in international trade, though some pathways remain more difficult to control and many species continue to be unintentionally introduced (E. Allen et al., 2017; Hulme, 2014; **Chapter 5**, **section 5.2.2**).

Trends

Reports on occurrences of alien species on cultivated land are usually restricted to plant pathogens, while more general comprehensive analyses of trends of alien species on cultivated areas are largely lacking. For alien species considered as plant pathogens, which mostly consist of arthropods, fungi and oocmycetes, the number of species has increased continuously since 1800 with a rise also in the rate of annual records until the present (Aukema et al., 2010; Kiritani & Morimoto, 2004; Nealis et al., 2016; R. M. Smith et al., 2018; F.-H. Wan & Yang, 2016). This is very likely a result of increased trade activity, particularly of plant materials, both in terms of increased volumes and increased geographic distances between donor and recipient regions. While the number of studies is geographically restricted to a few well-sampled regions, global analyses are missing; however, it is likely that alien species numbers have been increasing as observed in other world regions.

Status

Agricultural areas in Eastern Europe are the most invaded by alien plants of all European regions (Chytrý et al., 2009). On arable land there were on average 7.3±9.8 per cent of plant species introduced after 1500 in Catalonia (n=506), 5.6±5.2 per cent in the Czech Republic (n=1441) and 14.3±25.6 per cent in the United Kingdom (n=989); these values represent per centages of all plants recorded in vegetation plots 15–200 m^2 in size (Chytrý et al., 2008). For plants introduced from the beginning of Neolithic agriculture until 1500 (Pyšek & Jarošík, 2005), 55.5±13.5 per cent and 16.2±16.0 were reported for the Czech Republic and the United Kingdom, respectively (Chytrý et al., 2008).

Data from cultivated habitats in Europe comparing alien species of plants, insects, herptiles, birds and mammals introduced after 1500 showed that as a per cent of the total alien species in a region, cultivated habitats on average harbour 34 per cent of plants (based on 115 regional datasets:

median, with range 5–95 per cent), 46 per cent (26–66 per cent) of insects, 63 per cent (0–100 per cent) of herptiles, 65 per cent (51–85 per cent) of birds, and 30 per cent (0–100 per cent) of mammals (Pyšek, Bacher, et al., 2010). By this measure, cultivated habitats are among those with the highest levels of established alien species (Pyšek, Bacher, et al., 2010).

The domestication of plants and their widespread planting in agriculture has created unique resources that facilitate the establishment of new insect species (Liebhold et al., 2018). Across most continents, the historical expansion of plantings for agriculture and forestry has been followed by the invasion of insects that utilize these crop species as hosts (e.g., Hurley et al., 2016; Margaritopoulos et al., 2009).

Data and knowledge gaps

Information on biological invasions of insects and plants in cultivated areas has been systematically collected in Europe and North America, likely because they act as pests and weeds and negatively impact agricultural production. However, information from other parts of the world is scarce.

2.5.5.3. Aquaculture areas

Inland, coastal, and marine farming is largely based on introduced species and a large share of the industry occurs in South-East Asia and South America. In addition to being an important pathway of introduction for alien species, aquaculture facilities can also contain many pathogens, parasites, and fouling species unintentionally introduced as contaminants with the farmed species and the materials used for their production (e.g., K. E. Costello et al., 2021; Peeler et al., 2011). Molluscs can carry many non-target species with them: for example, several introduced marine algal alien species worldwide were transported in association with mariculture, mainly of molluscs (Mckindsey et al., 2007). In Europe, the production of native oyster *Ostrea edulis* (European oyster) has been greatly impacted by the parasite protozoan *Bonamia ostreae*, one of the diseases notifiable to the World Organisation for Animal Health (WOAH, founded as OIE; Carnegie & Cochennec-Laureau, 2004), and also by the parasitic copepod *Myicola ostreae*, both introduced together with *Magallana gigas* (Pacific oyster) (K. E. Costello et al., 2021). Two bivalves (*Magallana gigas*, and *Ruditapes philippinarum* (Japanese carpet shell)) were responsible for the majority of introductions of contaminants in Europe (60 species), mainly shell foulants or macroalgae used for packaging live oysters and clams (Savini et al., 2010). The aquaculture of *Magallana gigas* is likely responsible of the introduction of *Styela clava* (Asian tunicate) in New Zealand, which poses a threat to the shellfish aquaculture industry (Forrest et al., 2011). Many alien species introduced for aquaculture have escaped from confined systems, established, and become invasive (Ju et al., 2020): for example, the analysis of both marine and estuarine species in California showed that 106 of 126 (84 per cent) introductions were due to aquaculture and led to established populations of alien bivalves (K. E. Costello et al., 2021).

Trends

Worldwide, the introduction of alien species in aquaculture is well-known, but the numbers have significantly increased since the 1950s with technological improvements (i.e., development of artificial propagation, (Shelton & Rothbard, 2006)). Other notable increases were reported in the 1960s and 1970s with the movement of *Tilapia* spp. (tilapia) and *Oreochromis* spp. (tilapia). In the 1990s Asian carp (e.g., *Ctenopharyngodon idella* (grass carp), *Hypophthalmichthys nobilis* (bighead carp), *Hypophthalmichthys molitrix* (silver carp)) was used to meet the growing demand of food to reduce the harvesting of wild species and to diversify the production (De Silva, 2012; De Silva et al., 2006; Naylor et al., 2001; Shelton & Rothbard, 2006). This increasing trend is consistent across the continents (FAO, 2020), particularly in Asia. China, for example, has experienced a notable increase of alien species farmed in aquaculture mostly in the 1990s, even

though the introductions started in the 1920s (Casal, 2006; Cook et al., 2008; Y. Lin et al., 2015; J. Liu & Li, 2010; Q. Wang et al., 2015; Xiong et al., 2015, 2017). A similar increase was reported for Europe beginning in the 1970s (Olenin et al., 2008; Savini et al., 2010; Turchini & De Silva, 2008), and in the Americas (Gozlan, 2008), especially in Latin America and the Caribbean since the 1970s-1980s with the introduction of salmonids, tilapia, Asian carps and shrimps (Shelton & Rothbard, 2006). In the United States, many native species are cultured for food, and tilapia and Asian carp introduction for food production began in the 1950-60s (Shelton & Rothbard, 2006). In Africa, aquaculture production increased since the 1980s (Shelton & Rothbard, 2006), relying mainly on introduced Asian carp and African tilapia moved within the African continent (Bartley & Marttin, 2004). In Africa, three waves of fish introductions (a total of 139 species, 40 per cent for aquaculture) occurred: before 1949, between 1950-1989, and after 1990 (Satia & Bartley, 1998). In Oceania, even though few alien species were introduced for aquaculture since 1900, this region began having an important position in aquaculture production during the 1970s (Gozlan, 2008), with alien species making up 38 per cent of the production on average (Cook et al., 2008). Overall, aquaculture is mainly for food production. However, the market for ornamental and angling species is increasing, especially in Asia, Europe, and North America, thus increasing aquaculture-based introductions for this purpose (reviewed in Gozlan, 2008). Indeed, in the United States, more than half of the 91 fish species introduced through aquaculture are ornamental (J. E. Hill, 2008).

Fish, molluscs, and crustaceans are the most introduced taxonomic groups in aquaculture. Aquaculture is responsible for the majority of fish introductions globally (De Silva et al., 2009; Teletchea, 2019), as confirmed by the positive correlation shown between aquaculture production and the number of fish species introduced to a region (Gozlan, 2008). Overall, the introductions of fish started before the other groups, with a first "wave" before 1900, followed by other waves in the early 1900, after 1950 and after 1960s-70s (Shelton & Rothbard, 2006): Casal (2006), extracting the data of FishBase, reported 3072 fish introductions involving 568 species, with aquaculture being the main reason of introduction (40 per cent), while in 2008, Gozlan (2008) mentioned 624 fish species introduced worldwide, 51 per cent of them for aquaculture. Freshwater fish, particularly *Cyprinus carpio* (common carp), tilapia (specifically *Oreochromis niloticus* (Nile tilapia) is the main farmed tilapia), *Salmo trutta* (brown trout), and *Oncorhynchus mykiss* (rainbow trout) are the most introduced for aquaculture production (De Silva, 2012; Teletchea, 2019). Only 15 marine fish have been introduced for aquaculture (Atalah & Sanchez-Jerez, 2020). In contrast, all molluscs introduced for aquaculture are marine (19 species reported in (De Silva, 2012; X. Guo, 2009), with *Magallana gigas* (Pacific oyster) being one of the most successfully introduced aquatic alien species throughout the world since the end of nineteenth century in United States, Canada, Europe, Australia, New Zealand, Mexico, Peru, Chile, Argentina, and South Africa (De Silva, 2012; X. Guo, 2009). The other alien mollusc species were mostly introduced in the 1960s and from the 1980s (X. Guo, 2009). In the last twenty years, the most widely introduced alien species were reported from the eastern Pacific, such as *Penaeus vannamei* (whiteleg shrimp) reported by Fernández de Alaiza García Madrigal et al. (2018); in 2013, its production of 4.3 million tons represented 64 per cent of the global farmed shrimp production. Finally, since the 1970s, many alien seaweeds have been unintentionally introduced through aquaculture, while very few species were intentionally introduced for production (FAO, 2020; Pickering et al., 2007).

Status

Asia is considered the "backbone of global aquaculture production" (De Silva, 2012) with its contribution to over 90 per cent to the sector (De Silva et al., 2009); aquaculture heavily relies on alien species (De Silva et al., 2006, 2009; Ju et al., 2020), particularly, in China, the leading global aquaculture producer (more than 60 per cent of the global production, Cao et al., 2015; Q. Wang et al., 2015). In China, alien species (a total of 179 species, Y. Lin et al., 2015) are involved for over 25 per cent of the total production (Xiong et al., 2017), compared to the 17 per cent of global production of alien species (Shelton & Rothbard, 2006). Asia also stands out for the widely cultured

species of *Penaeus vannamei* (whiteleg shrimp), introduced in 1978 in Asia, with contributions from China, Thailand, Indonesia, and Vietnam to most of the world's shrimp production (Liao & Chien, 2011). In Europe, at least 703 alien species introduced to aquatic ecosystems for aquaculture and stocking activities have been reported: fish, crustaceans and molluscs are the most introduced taxonomic groups (Olenin et al., 2008; Savini et al., 2010; Teletchea, 2019; Turchini & De Silva, 2008). In Europe, alien species (mostly *Oncorhynchus mykiss* (rainbow trout), *Hypophthalmichthys molitri* (silver carp) and *Cyprinus carpio* (common carp)) contributed 67 per cent of freshwater aquaculture production, mainly in Western areas with a range of 88-98 per cent (Turchini & De Silva, 2008). The highest production of introduced marine fish is concentrated in the Magellanic province of southern Chile that is considered at risk of environmental impacts caused by escapees from the confined environment (Atalah & Sanchez-Jerez, 2020). Recent planning for diversification in aquaculture reports advised for a shift towards producing more native than alien species (Harvey et al., 2017).

The worst impacts on aquaculture production have been caused by the oomycete *Aphanomyces astaci*, the causative agent of the crayfish plague. Vectored by North American crayfish introduced to Europe for aquaculture, this plague dramatically reduced native populations and the production of native European crayfish (De Silva et al., 2009). Many pathogens can also be carried by alien finfish, especially cyprinids: at least 226 parasite species (34 of which causing important diseases worldwide) have been found in *Cyprinus carpio* (common carp), one of the most introduced alien species (Jeney & Jeney, 1995). In Europe, the seven most farmed cyprinids led to the introduction of 31parasites⁄disease agents (Savini et al., 2010). Similarly, in South Africa many parasites have been introduced with fish and crayfish used for fisheries and aquaculture (Weyl et al., 2020). Despite the high number of pathogens transferred by alien farmed fish, a large-scale mass mortality of farmed fish due to introduction of associated pathogens has not yet been recorded (De Silva et al., 2009). Still, alien farmed shrimps can carry several diseases that lead to important outbreaks in the facilities and relevant economic losses, especially in Asia (Briggs et al., 2004).

Data and knowledge gaps

The Food and Agriculture Organization (FAO) Database on Introductions of Aquatic Species (DIAS) (FAO, 2021) reports the introduction of alien species per country, providing also global maps of species introduced for aquaculture and a focus on some alien species, such as *Cyprinus carpio* (common carp) and *Oreochromis niloticus* (Nile tilapia). In general, there is considerable information available for Asia, the leading continent for aquaculture production, and for Europe and Latin America while for other regions information is often lacking. Recent reviews addressed fish, molluscs and shrimp situations. Studies on temporal trends are limited and mainly available for the three main taxonomic groups fish, molluscs, and crustaceans.

2.5.5.4. Coastal areas intensively used for multiple purposes by humans

Trends

Accumulation rates of established alien species in coastal marine waters frequently show a pattern of exponential accumulation through time, with the number of new reports increasing dramatically during the last 30 years with increased awareness and research effort (Bailey et al., 2020; Leppäkoski et al., 2002; Ruiz et al., 2015). The earliest substantiated reports of established alien marine species date to at least the 1200s (Ojaveer et al., 2018). The type of transported taxa has changed over time as shipping pathways have modernized. For example, historical use of solid ballast, such as rocks, sand, and dirt, was associated with the transportation of seeds and insects while the modern use of seawater ballast correlates with introductions of aquatic taxa ranging from microbes and protists to macroinvertebrates and fishes (Bailey, 2015). There are also now fewer intentional introductions of fishes and macroinvertebrates into the natural environment, likely

because the potential negative impacts of such releases are now better understood (Bailey et al., 2020).

While the rate of new alien species records has levelled off and even declined since 2010, possibly due to regulations for ships' ballast water and improved practices by the aquaculture industry (Bailey et al., 2020; **Chapter 5**, **section 5.51**), expectations of continued global shipping growth suggest the risks of biological invasions could increase significantly by 2050 without management of shipping-mediated vectors (Sardain et al., 2019) thus underscoring the importance of existing instruments to prevent introductions via ballast water and biofouling. The construction and successive enlargement of canals connecting previously unconnected waterbodies has been responsible for a growing number of established alien species in the Mediterranean (Galil et al., 2017). Similarly, it has been projected that the recent expansion of the Panama Canal could triple the number of established alien species arriving in the Gulf of Mexico and the North American East Coast (Muirhead et al., 2015). In regions such as the Arctic, the changing environmental conditions and the dramatic increase in shipping activity are likely to favour the transport and introduction of new alien species. This increase in alien species is likely to reconfigure the global dynamics of invasive alien species, potentially reshaping marine habitats and ecosystem functions, especially in coastal regions (Goldsmit et al., 2020; Miller & Ruiz, 2014).

Status

There has been extensive research and surveillance of coastal marine alien species in Central and Western Europe, with more than 4,350 detection records for at least 1,370 introduced species of alien or unknown (cryptogenic) origin (AquaNIS, 2015). More than 450 marine alien species have been recorded off the Israeli Mediterranean coast – which serves as a gateway for introductions from the western Indian Ocean and Red Sea, through the Suez Canal, to the Mediterranean Sea (Galil et al., 2021a).

Coastal areas are generally prone to biological invasions. In a global study of established alien species richness of a number of taxonomic groups, Dawson et al. (2017) found that hotspots are, other than islands, predominantly coastal mainland regions.

In the Americas, at least 450 alien species are reported from continental North America (Ruiz et al., 2015), and approximately 300 other species from Hawaii (Carlton & Eldredge, 2009). Reported numbers are lower in South America, with 129, 138, and 53 species reported from the south-west Atlantic, Brazil, and the Galápagos Islands, respectively (Carlton et al., 2019; Schwindt et al., 2020; Teixeira & Creed, 2020). Despite the low number of reported alien species, the coastal environments of the south-west Atlantic were affected by one of the largest continental-scale bioinvasion events ever recorded, and which has reshaped vast coastal-marine ecosystems, modifying their coastal geomorphology, biodiversity, primary and secondary productivity in the Americas and Asia (Bortolus et al., 2015, 2019; Qiu, 2013). Researchers have shown that what are now extensive *Sporobolus alterniflorus* (smooth cordgrass) marshes in this region, were probably bare mudflats centuries ago, and that the *Sporobolus alterniflorus* introduction might have led to vast unrecorded shifts in bird, fish, and invertebrate biodiversity, and immense shifts in algal vs. detritus production, with the concomitant trophic cascades that these changes imply (Bortolus et al., 2015, 2019). Reports of mudflat conversion by *Sporobolus alterniflorus* with distinct ecological consequences have also been reported from China (B. Li et al., 2009). Similarly, the coastal systems of North America have been transformed by an introduced genotype of the macrophyte *Phragmites australis* (common reed) causing whole ecosystem and habitat transformations (Bowen et al., 2017; Chambers et al., 1999; Cronin et al., 2015; Dibble & Meyerson, 2014).

In the Asia-Pacific region, at least 650 marine alien and cryptogenic species are reported from New Zealand (Seaward & Inglis, 2018), with another 343 introduced and cryptogenic species reported

from Australia (Sliwa et al., 2008), and 213 alien species reported from China (Xiong et al., 2017). At least 95 alien and 39 cryptogenic species are reported from South Africa (T. B. Robinson et al., 2016), with most of the African continent being understudied.

From1965-2015, at least 1,400 unique alien species have been reported as being introduced in coastal ecosystems – approximately one new species detected every 8 days for the last fifty years (Bailey et al., 2020).

Data and knowledge gaps

Records of alien species in coastal environments are more reliable in recent decades as the awareness of alien species introductions and their potential negative impacts began to increase. However, data are still limited for many taxonomic groups and regions of the world (especially Africa, Meso- and South America and Asia) (Bailey et al., 2020). Aquatic alien species are frequently under-reported due to limited research intensity and insufficient taxonomic expertise (especially for smaller-bodied organisms) (Carlton & Fowler, 2018; Ojaveer et al., 2017). Reliable records of alien species introductions exist mainly for plants and animals, with fungi, protists, and microbes generally being understudied.

An accurate number of alien species introduced across global coastal waters is difficult to estimate since organisms were being transported around the world by ships for centuries before inventories of species in the marine environment, resulting in an inability to determine the true origin of a large proportion of species within coastal communities (Bortolus et al., 2015; Carlton, 1996; Hewitt et al., 2004; Schwindt et al., 2020). There can also be long time lags after the initial introduction and establishment of a new population until its discovery (C. J. Costello & Solow, 2003; C. M. Taylor & Hastings, 2005), unless regular and targeted monitoring is taking place (Hayes et al., 2019). In many regions of the world, regular surveillance is hampered by inadequate resources and limited access to taxonomic expertise (Ojaveer et al., 2014). The number of alien introductions is therefore certainly much higher than published literature suggests.

The study of invasive alien vascular plant species introduced in the marine-coastal environments of South America is currently one of the largest gaps to cope with. Besides a few classic examples including genera such as *Tamarix* (tamarisk), *Carpobrotus*, *Ammophila*, *Sporobolus*, or *Salsola* (Schwindt et al., 2018), there is little research effort in this area and no updated review or synthesis revising the list of plant invasive alien species for this region. Large regions like South America have invested little effort (e.g., relative to Europe or North America) to recording and monitoring the introduction of alien species. This lack of data has often been misunderstood as an actual lack of invasive alien species. This knowledge gap seriously hampers the ability to recognize pre-existing native ecosystems (i.e., Ecological Mirage Hypothesis; Bortolus et al., 2015; Bortolus & Schwindt, 2007). On the other hand, there is currently an increase in the number of researchers investigating invasive alien species in this region (Schwindt & Bortolus, 2017), which will likely increase the number of reports of introduced species for the region. Nevertheless, this increase is not necessarily, or strictly, due to new introductions, but could also include introductions long overlooked and ignored. For instance, in 2017 scientists found that what was until then considered a native alga, *Melanothamnus harveyi* (Harvey's siphon weed), was in fact the earliest record of an alien coastal marine species for the region, being first reported in 1872 under the name of *Polysiphonia argentinica* (Schwindt et al., 2020). Similarly, *Sporobolus alterniflorus* (smooth cordgrass) was recognized as alien to the southern Atlantic coastal environments by 2015, nearly two centuries after its introduction (Bortolus et al., 2015).

Finally, the lack of research on emerging or understudied transportation pathways, such as the aquarium and bait trades, internet commerce and anthropogenic marine litter (e.g., M. L. Campbell et al., 2017; J. T. Carlton et al., 2017; Fowler et al., 2016; Lenda et al., 2014), likely results in gaps

of knowledge. This knowledge gap refers to the relative importance of different introduction mechanisms and the corresponding management priorities for reduction of future introductions of aquatic alien species.

Box 2.11. Good Quality of Life: A global assessment of trends and status of invasive alien species

Invasive alien species are a significant and growing threat worldwide to the good quality of life (i.e., the achievement of a fulfilled human life, see IPBES glossary[6] for a complete definition) for many communities (Costanza et al., 2006). A literature review conducted by the authors of **Chapter 4** identified about 1050 invasive alien species that impact good quality of life (**Chapter 4**, **Figure 4.2**). In most cases (841 cases), the reported impacts negatively affected good quality of life, while in 212 cases, benefits of invasive alien species were reported. However, it is critical to note that a benefit from an invasive alien species in one sector does not mitigate the harm caused elsewhere, and that the same invasive alien species may both cause harm and produce a benefit. Integrating this invasive alien species list and the distributional data provided in this chapter (**section 2.1.4** for data details) reveals that the United States, Australia, New Zealand, multiple European countries, China, Japan, Canada, Mexico, and South Africa were the countries with highest numbers of invasive alien species with impacts (negative or positive) on the good quality of life (**Figure 2.36**). This pattern largely reflects the distribution of all identified alien species (**Figure 2.5**) suggesting that in general, more impacts on good quality of life have been reported where more alien species were found.

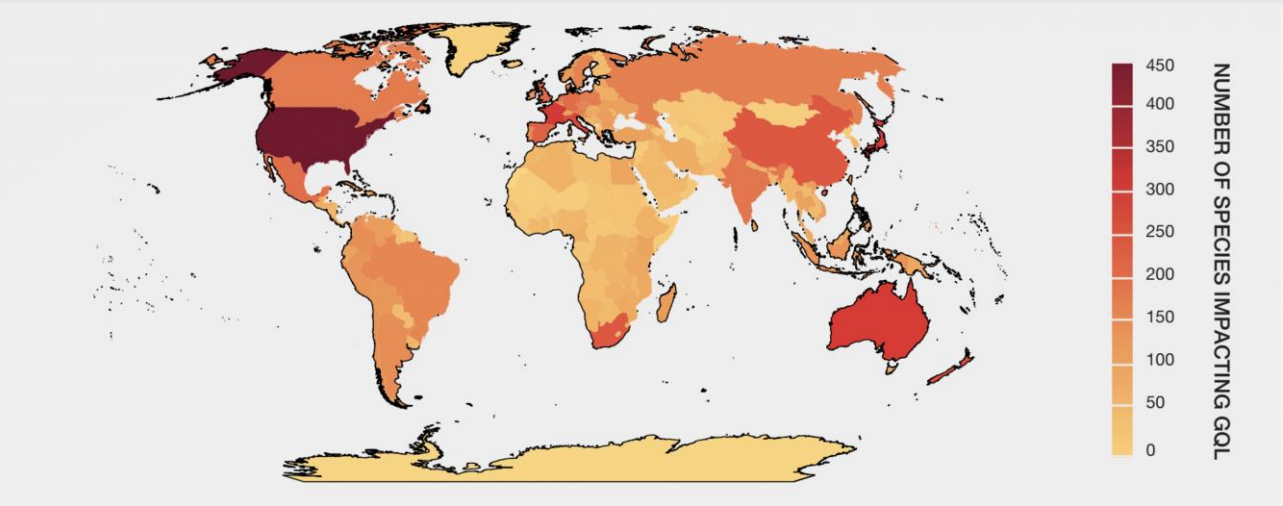

Figure 2.36. Map of invasive alien species numbers with reported impacts on good quality of life. Species were identified through the literature review conducted by Chapter 4 of this assessment (data management report available at: https:/doi.org/10.5281/zenodo.5766069) and the distributions of these species were extracted from the database used in **Chapter 2** (**section 2.1.4** for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582

The total number of invasive alien species with impacts on good quality of life has risen continuously at a nearly linear rate since around 1830 (**Figure 2.37**). During this time, the rate of increase remained relatively constant at around 15 new invasive alien species with impacts on good quality of life per five years (or three new species annually).

[6] IPBES glossary: https://ipbes.net/glossary

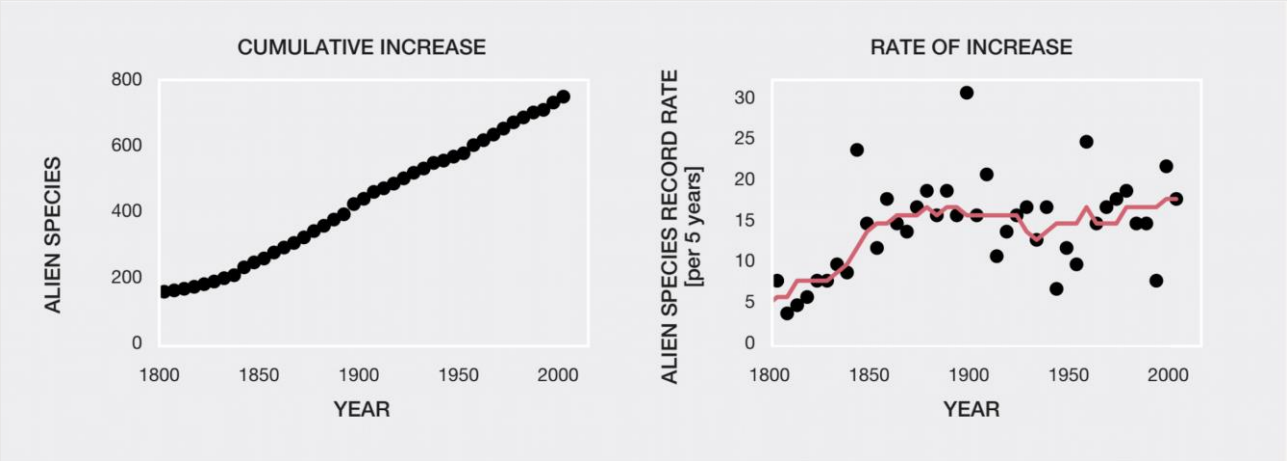

Figure 2.37. Trends in numbers of invasive alien species with reported impacts on good quality of life. Trends are shown as cumulative numbers (left panel) and as rate of increase (i.e., numbers of species per five years) (right panel). The smoothed trend (line) is calculated as running median (section 2.1.4 for further details about data sources and data processing). Species were identified through the literature review conducted by Chapter 4 of this assessment (data management report available at: https:/doi.org/10.5281/zenodo.5766069) and the trends for these species were extracted from the database used in Chapter 2 (section 2.1.4 for further details about data sources and data processing). Note numbers presented may deviate from those reported in the text due to variation among data sources. A data management report for the data underlying this figure is available at https://doi.org/10.5281/zenodo.7615582.

Most invasive alien species with impacts on good quality of life were insects (38 per cent), followed by vascular plants (29 per cent), fishes (7 per cent), molluscs (5 per cent), and mammals (5 per cent). Numerous widespread, well-known invasive alien species often negatively affect various aspects of good quality of life including culture, human health, and the local economy. High profile examples include fish species of the genus Oncorhynchus (trout and salmon) that have been introduced in many parts of the world (Crawford & Muir, 2008) and have changed local economies and livelihoods in areas. Such impacts include hybridization with native species and predation of native fishes (Kitano, 2004; Soto et al., 2001; Woodford & Impson, 2004). The introduction of Lates niloticus (Nile perch) has changed the local socio-economic dynamics such as a decline in multi-fisheries subsistence and livelihood (Njiru et al., 2018). In particular, women from marginalized communities have been disadvantaged by the effects of *Lates niloticus* on subsistence cichlid-based fisheries, and have had to adopt new livelihood practices, with prostitution being a primary one. This has, in turn, spurred inequality, social conflict, health issues (spread of human immunodeficiency virus (HIV) in particular), the loss of cultural practices, and reduced food security for local communities, thus affecting human well-being (R. T. Shackleton et al., 2018).

Another prominent example for an invasive alien species with impacts on good quality of life is Spodoptera frugiperda (fall armyworm). This alien insect pest has been spreading for decades and has wide-ranging impacts in many parts of the world including economic losses from reduced maize crop yields (Dassou et al., 2021; De Groote et al., 2020) and reduced local livelihood potential (Kassie et al., 2020). The species is likely to spread further due to suitable climatic conditions (Day et al., 2017; Early et al., 2018). As another example, Prosopis spp. (mesquite) is one of the most widely distributed invasive tree species globally. These species have invaded many arid and semi-arid parts of the world, thereby reducing water available for humans and animals (Bekele et al., 2018; Shiferaw et al., 2021), impacting human health via allergies, asthma, and physical injuries (Al-Frayh et al., 1999; Mwangi & Swallow, 2008), increasing malaria prevalence due to habitat provision (Muller et al., 2017), reducing grazing capacity (S. Kumar & Mathur, 2014; Mwangi & Swallow, 2008; Ndhlovu

et al., 2011), and impacting local economies through increased management costs and loss of grazing (R. T. Shackleton et al., 2014).

Focusing more specifically on Indigenous Peoples and local communities (i.e., typically ethnic groups who are descended from and identify with the original inhabitants of a given region; IPBES glossary[7]) and good quality of life, the assessment identified and assessed 131 regional case studies worldwide of the impacts of invasive alien species on the good quality of life and their effects for Indigenous Peoples and local communities. The most frequently reported species in the case studies were first identified, then species and their impacts on good quality of life concerning taxonomic groups, units of analyses, and IPBES regions. The findings suggested that the biggest impacts were from plant species (85 species, 65 per cent), of which most (79 species) were woody vascular plants.

The three most frequently reported invasive alien plants (38 cases) included either alone or in combination with other species were: Lantana camara (lantana), Prosopis spp., and Chromolaena odorata (Siam weed). Aquatic invasive alien plant species were reported in only six case studies. These included Pontederia crassipes (water hyacinth), Phragmites australis (common reed), Hydrilla verticillate (hydrilla), and Cryptostegia grandiflora (rubber vine), amongst others. Overall, fewer case studies (46 case studies) reported invasive alien species' impact on good quality of life for other taxonomic groups. These taxa included fish species (10 species) such as Cyprinus carpio (common carp), Tilapia rendalli (redbreast tilapia), Oreochromis mossambicus (Mozambique tilapia), and Lates niloticus, Oncorhynchus mykiss (rainbow trout). Insects (12 studies), were also reported including Spodoptera frugiperda, and Agrilus planipennis (emerald ash borer). Other taxa were not reported in any case studies.

The majority of case studies (60 per cent; 79 case studies) reported negative impacts of invasive alien species, while others reported both negative and positive impacts. Examples include Opuntia ficus-indica (prickly pear), which is used for fodder and fence lines but has thorns that cause injury to humans and animals (S. E. Shackleton & Shackleton, 2018). Positive impacts of invasive alien species include feral pigs that provide meat (C. J. Robinson & Wallington, 2012), woody plants (e.g., Acacia, Prosopis, Eucalyptus) that provide biomass for compost, timber and wood charcoal production (Rogers et al., 2017; Tassin et al., 2012; B. W. van Wilgen, 2012), shade (S. E. Shackleton & Shackleton, 2018), products to sell (Tilahun et al., 2017), and medicinal benefits (Witt et al., 2019). Despite the benefits provided, the positive impacts of invasive alien species on good quality of life do not counteract their negative impacts.

Knowledge and data gaps

There were large differences in the number of studies from the different IPBES regions potentially representing knowledge and data gaps on the effects of invasive alien species on good quality of life. Asia and the Pacific had the most studies (54), followed by Africa (44), the Americas (28), and Europe and Central Asia (3). There appears to be a bias in case studies towards reporting the effects of invasive alien woody vascular plants (65 per cent) on good quality of life since there were many fewer case studies on other widespread alien species groups, particularly invertebrates, microbes, and mammals (5 per cent).

[7] IPBES glossary: https://ipbes.net/glossary

2.6. Future dynamics of biological invasions

This section reports on the projected future dynamics of the trends and distribution of alien and invasive alien animal species in general (**section 2.6.1**), for animals (**section 2.6.2**), plants (**section 2.6.3**), and microorganisms (**section 2.6.4**), and addresses limitations for assessing future dynamics of biological invasions (**section 2.6.5**).

2.6.1. Overview of future dynamics of biological invasions

Recent increases in data availability and accessibility provide an improved baseline understanding of historic and current alien species richness and distributions that help to make new and improved projections (E. E. Dyer, Cassey, et al., 2017; Pagad et al., 2022; Seebens, Blackburn, et al., 2017; van Kleunen et al., 2019). However, many gaps still exist at the regional and taxonomic scales (Pyšek et al., 2008). Approaches to forecast dynamics of biological invasions vary, including expert-based systems (e.g., based on individual experts in their field, Indigenous and local knowledge systems (**Glossary**), horizon scanning approaches), various modelling approaches (e.g., expert-based models, correlative models, process-based models, hybrid models; **Chapter 1, section 1.6.7.3**) or scenario approaches (exploratory scenarios, target-seeking scenarios, policy-screening scenarios; **Chapter 1, section 1.6.7.3**).

Generally, prediction and projection studies have been conducted from regional, continental to global scales (Bellard, Thuiller, et al., 2013; Dullinger et al., 2017) illustrating the potential current and future numbers and distribution of alien species. Studies cover one to multiple species within (e.g., cacti: Masocha & Dube, 2018; termites: Buczkowski & Bertelsmeier, 2017; ants: Bertelsmeier et al., 2015, 2016; Fournier et al., 2019) and across taxonomic groups (e.g., the 100 worst invaders globally as assessed by the IUCN ISSG: Bellard, Thuiller, et al., 2013; Gallardo et al., 2017).

On the global scale, quantitative projections of established alien species numbers under a business-as-usual scenario do exist for the period from 2005–2050 (Seebens, Bacher, et al., 2021). For seven major taxonomic groups established alien species numbers are projected to increase across eight continental regions (**Figure 2.38**). At the continental scale, the strongest relative increase in established alien species numbers of 64 per cent (2,543 ± 237 species) is expected for Europe, followed by temperate Asia (50 per cent; 1597 ± 197) and South America (49 per cent; 1,391 ± 258). Globally, an average relative increase of 36 per cent, equivalent to 1,195 ± 131 new established alien species is projected (Seebens, Bacher, et al., 2021). A list of relative and absolute projected increases of established alien species numbers until 2050 is given in **Table 2.28**. However, given the projected acceleration of the majority of direct and indirect drivers of change in nature, it is likely that the numbers of established alien species will be higher than those predicted in the business-as-usual scenario (**Table 2.28**). Comparing past and future trends, the rate of increase of established alien species numbers is expected to increase even further (i.e., acceleration) for arthropods and – to a lower degree – birds worldwide. In contrast, rates are projected to decline for mammals globally and partly for fishes, although rates are still positive, resulting in more alien species, but at a lower rate than observed before (Seebens, Bacher, et al., 2021). However, the number of alien and invasive alien species is expected to rise even without the introduction of any new species by humans, because the majority of already established alien species are still spreading (Seebens, Blackburn, et al., 2021). Thus, already established alien species are likely to spread further also to neighbouring regions, which will result in further increases in alien species numbers regionally.

A literature review[8] on studies including models and scenarios of biological invasions shows that the current literature is dominated by correlative model approaches (57 per cent) and correlative scenarios (87 per cent) and that these studies mainly explore either long-term (2050-2100) or short-term (until 2030) trends (42 per cent and 30 per cent respectively) (**Chapter 1, section 1.6.7.3**).

The remainder of this section provides an overview of the general trends of predicted and projected alien species richness and distributions for different taxonomic groups and across scales.

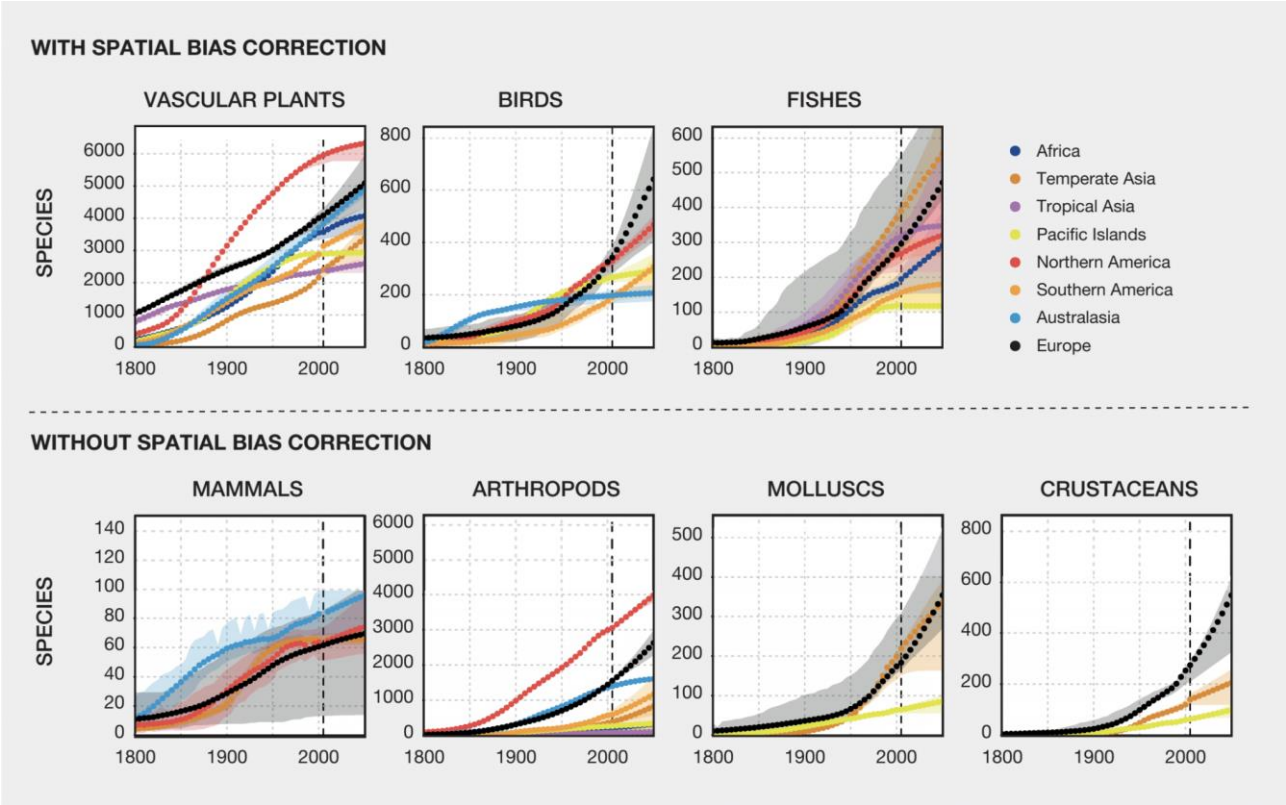

Figure 2.38. Projected trends of established alien species numbers until 2050. Projections are shown for seven major taxonomic groups across eight global regions and based on a business-as-usual scenario that assumes that drivers facilitating biological invasions will develop in the future as has been observed during recent decades. For vascular plants, birds, and fishes a spatial bias correction was applied to account for spatial heterogeneity in data availability. This was not possible for the other taxonomic groups due to data deficiency. Trend lines show averaged trends out of repeated simulations, while variation around the means is indicated by shaded areas. From Seebens et al. (2021), https://doi.org/10.1111/gcb.15333, under license CC BY 4.0.

Table 2.28. Projected relative (per cent) increases of established alien species numbers until 2050

Projections are representative for a business-as-usual scenario, assuming similar developments in drivers facilitating biological invasions as observed in the past. Values are mean estimates over 100 model runs with the upper and lower 2.5 per cent confidence interval given in square brackets. The absolute established alien species numbers increase averaged more than 100 model runs are provided in round brackets together with the standard deviation estimates. Data are from Seebens, Bacher, et al. (2021).

	Africa	Australasia	Europe	Northern America	Pacific Islands	South America	Temperate Asia	Tropical Asia

[8] Data management report available at: https://doi.org/10.5281/zenodo.5706520

Mammals		14 [2, 29] (12±3)	13 [0, 167] (8±9)	16 [1, 46] (10±9)			0 [0, 10] (0±1)	
Birds	42 [0, 75] (59±26)	5 [1, 9] (9±4)	88 [44, 139] (299±53)	42 [32, 46] (138±11)	9 [1, 29] (24±22)	60 [10, 70] (115±20)		67 [36, 91] (78±15)
Fishes	49 [1, 75] (96±39)		59 [37, 104] (175±32)	20 [2, 70] (54±57)	0 [0, 1] (0±0)	16 [1, 96] (25±39)	42 [7, 62] (165±48)	10 [0, 76] (31±34)
Arthropods	51 [0, 73] (109±51)	15 [13, 18] (212±14)	69 [48, 85] (1072±92)	30 [24, 34] (927±31)	26 [1, 35] (70±17)	99 [0, 130] (582±249)	117 [57, 145] (445±87)	35 [0, 58] (24±13)
Molluscs			93 [59, 135] (170±31)		32 [2, 47] (21±7)		53 [3, 73] (116±40)	
Crustaceans			100 [51, 117] (273±34)		56 [10, 90] (36±8)		47 [0, 76] (66±18)	
Vascular plants	14 [4, 19] (503±113)	28 [22, 29] (1065±41)	24 [16, 39] (997±209)	6 [1, 7] (365±33)	1 [0, 2] (38±9)	21 [18, 25] (669±52)	41 [28, 54] (987±170)	10 [0, 17] (227±67)

2.6.2. Animals

For some bird species, such as *Corvus splendens* (house crow) and *Acridotheres tristis* (common myna), the current distributions indicate a large potential to spread to new areas (Magory Cohen et al., 2019; Nyári et al., 2006). Similarly, mammals such as *Sus scrofa* (feral pig), *Herpestes javanicus auropunctatus* (small Indian mongoose), and *Procyon lotor* (raccoon) often have a large potential of future invasions worldwide (Lewis et al., 2017; Louppe et al., 2019, 2020). In the marine realm, a study of 19 ascidian species finds a large invasion potential especially at higher latitudes (Lins et al., 2018). For insects, several studies investigated the invasion potential of agricultural pest species (e.g., *Phthorimaea operculella* (potato tuber moth) (Kroschel et al., 2013), *Bactrocera carambolae* (carambola fruit fly) (Marchioro, 2016), *Diabrotica* spp. (e.g., cucumber beetles) (Marchioro & Krechemer, 2018), *Bemisia tabaci* (tocacco whitefly) (Ramos et al., 2018), *Spodoptera frugiperda* (fall armyworm) (Early et al., 2018), *Halyomorpha halys* (brown marmorated stink bug) (Kriticos et al., 2017), *Drosophila suzukii* (spotted wing drosophila) (L. A. dos Santos et al., 2017)), and all studies found a high risk of invasion beyond the current realized distribution. Although less investigated, high invasion potentials have also been identified for other insect species (e.g., Fournier et al., 2019; He et al., 2012; H. Li et al., 2006; Peacock & Worner, 2006). A study on the potential biological invasion risk of protected areas worldwide found that 95 per cent of the protected areas have high habitat suitability for alien mammal species across 11 taxonomic groups (X. Liu et al., 2020).

An analysis of the 100 worst invaders of the world (as assessed by the IUCN ISSG) found a decreased potential for future global distribution of mammals, birds, fishes, reptiles, and amphibians, but an increase in distributions of aquatic and terrestrial invertebrates due to region specific projected changes in climate and land-use, using an ensemble species distribution models approach (Bellard, Leclerc, et al., 2013). Other global and regional studies have focused on the future invasion potential for species from different taxonomic groups such as ants and termites (projected increases for 12 out of 13 species; e.g., Bertelsmeier et al., 2013b, 2015; Buczkowski & Bertelsmeier, 2017; Y. Chen, 2008), beetles (projected increase; e.g., Berzitis et al., 2014; Kistner-

Thomas, 2019; C. Wang et al., 2017), flies (northward shift and decrease in global suitability; e.g., Capinha et al., 2014; M. P. Hill et al., 2016; Qin, 2019; S. F. Ryan et al., 2019), other insects (projected increase; e.g., M. P. Hill et al., 2017; Lu et al., 2020), amphibians (projected stable distribution or increase; e.g., Ficetola et al., 2010; Forti et al., 2017; Ihlow et al., 2016), fish (projected increase; e.g., Dong et al., 2020; Kramer et al., 2017) and mammals (projected increase; e.g., Louppe et al., 2019, 2020).

Under different scenarios of change of the global shipping network, which constitutes a major driver responsible for biological invasions (**Chapter 3, section 3.2.3.1**), and across taxonomic groups, high invasion risks have been identified for Asia and Europe (especially the Mediterranean) with a projected significant increase in the global invasion risk without management of shipping-mediated vectors (Sardain et al., 2019). A risk assessment in the 19 Arctic ecoregions identified hotspots of future invasion for 23 invasive planktonic and benthic species in Hudson Bay, Northern Grand Banks/Labrador, Chukchi/Eastern Bering Seas and Barents/White Seas (Goldsmit et al., 2020). Contrary to the projected Arctic expansion of the species their global projected range contracted, indicating a northward shift of future invasions (Goldsmit et al., 2020). Mammal species, such as *Procyon lotor* (raccoon) and *Herpestes javanicus auropunctatus* (small Indian mongoose), are expected to shift to higher latitudes (Louppe et al., 2019, 2020). Studies of individual fish species project potential future invasion risk across continents and at the regional scale (Dong et al., 2020; Kramer et al., 2017). For amphibians, two frog species (*Xenopus laevis* (African clawed frog) and *Lithobates catesbeianus* (American bullfrog)) are projected to have stable to decreasing future distributions under climate change (Ficetola et al., 2010; Ihlow et al., 2016). For insects, future potential distributions under climate change scenarios project poleward shifts (Capinha et al., 2014; M. P. Hill et al., 2016; Kistner-Thomas, 2019; Qin et al., 2019) with many species increasing their potential distributions (Bellard, Thuiller, et al., 2013; Bertelsmeier et al., 2015; Buczkowski & Bertelsmeier, 2017; Y. Chen, 2008; Lu et al., 2020; Qin et al., 2019). At the same time, some insect species' distributions (e.g., *Aedes aegypti* (yellow fever mosquito), *Pheidole megacephala* (big-headed ant)) are projected to decrease as well, with the declines mainly located in tropical regions (Bertelsmeier et al., 2013b; Capinha et al., 2014; S. J. Ryan et al., 2019).

In summary, the suite of studies available for projections of future dynamics of alien species suggests that overall ranges of alien species are expected to increase in most cases although with large variation due to a continuous introduction of new individuals and an expansion of ranges to other suitable habitats. In addition, ranges are expected to shift poleward because of global warming (Walther et al., 2009). The total number of alien species is expected to increase until 2050 for most investigated taxonomic groups such as birds, fishes, mammals, arthropods, molluscs, and crustaceans (Seebens, Bacher, et al., 2021). These trends are consistent across all continents except alien birds in Europe, alien mammals in tropical Asia, and alien fish on Pacific Islands, which are projected to reach a plateau. Relative increases between 2005 and 2050 range between 117 per cent (arthropods in temperate Asia) and 5 per cent (birds in Australasia) (Seebens, Bacher, et al., 2021).

2.6.3. Plants

Potential hotspots of alien plants have been identified by modelling the distribution of individual plant species and projecting the distribution under future environmental conditions. For the 100 worst invaders (as defined by the IUCN), Europe, northern North America, and Oceania emerge as potential hotspots for invasion (Bellard et al., 2016), while potential hotspots for cacti emerge in the Mediterranean, tropical savanna regions, and xeric shrubland biomes (Masocha & Dube, 2018). Other global studies on large sets of alien plant species identify high invasion risk in Europe, South America, North America, southwest China and New Zealand as well as the coast of West Africa and the southern coast of Asia (J.-Z. Wan et al., 2016; Y. Wang & Xu, 2016). Regions of high invasion risk change depending on the taxa under investigation. For 10 parasitic Orobanchaceae species tropical and subtropical regions are most suitable for potential future invasions (Mohamed

et al., 2006). Higher potential future suitability has also been projected along roadsides (Azan et al., 2015) and at the margins and buffer zones of protected areas (Gallardo et al., 2017; Paclibar & Tadiosa, 2019), while potential future biological invasion risk is lower inside protected areas (Gallardo et al., 2017; Paclibar & Tadiosa, 2019).

On the global scale, future distributions of some alien plant species are projected to expand (e.g., J.-Z. Wan et al., 2016), while others will contract in parts of their current range (e.g., range contractions mainly at lower latitudes; Bellard, Leclerc, et al., 2013) under different climate change scenarios. A recent study predicted the global distribution of 336 terrestrial invasive alien plants under future climate change scenarios (J.-Z. Wan et al., 2016). It identifies the main future invasion hotspots for plant invasions to be in South America, Europe, New Zealand, and northern and Southern Africa (J.-Z. Wan et al., 2016). Other studies focus either on single alien plant species (R. Ahmad et al., 2019; Bourdôt et al., 2012; Heshmati et al., 2019) or sets of species within specific regions (e.g., Adams et al., 2015; R. Ahmad et al., 2019; J. M. Allen & Bradley, 2016; Dullinger et al., 2017; Paclibar & Tadiosa, 2019). Most studies for Northern America and Europe report strong increases in overall potential future range sizes (e.g., Adhikari et al., 2015; J. M. Allen & Bradley, 2016; Dullinger et al., 2017) under global change, with the magnitude of change within these regions varying according to the species investigated and increases in suitable ranges are mainly directed towards higher latitudes (J. M. Allen & Bradley, 2016). Studies for the United States and Europe project that most current invasion hotspots will remain stable spatially, but potential invasion alien species richness will increase between 64 to 102 per cent (J. M. Allen & Bradley, 2016; Dullinger et al., 2017).

For Europe, a prediction of future development of plant invasions until 2080 under three socioeconomic scenarios differing in focus on economic growth vs. sustainability has been made based on data from vegetation plots (Chytrý et al., 2012). Under all scenarios an increase in the level of invasion was projected for north-western and northern Europe, and under two of the scenarios a decrease for some agricultural areas of Eastern Europe where abandonment of agricultural land is expected. However, the implementation of sustainability policies would not automatically restrict the spread of alien plants (Chytrý et al., 2012).

Following a business-as-usual scenario, thereby assuming that drivers will develop in the future as observed in the past, alien vascular plants species numbers are expected to increase steadily across all continents with only North America showing a weak sign of saturation by 2050 (Seebens, Bacher, et al., 2021; **Figure 2.38**). The range of the projected increase of alien vascular plants lies between 1 per cent (Pacific Islands) and 41 per cent (Temperate Asia) from 2005-2050 (**Table 2.28**). Likewise, relative increases in species numbers are projected to increase more strongly in aquatic than non-aquatic environments (Seebens, Bacher, et al., 2021). In the marine realm, future increases in alien algae species introductions are projected for Asia and Europe (Seebens, Bacher, et al., 2021) and mainly along the major shipping routes (Sardain et al., 2019).

2.6.4. Microorganisms

A recent review of species distribution models used for fungi has identified 75 studies predicting the potential distribution of fungi under current climates (Hao et al., 2020). The majority of studies deal with one species only or with multiple species from the same genus (e.g., *Phytophthora*; Scott et al., 2019) and generally invasion risk is predicted to be higher as currently observed, both in terms of numbers of alien fungi present (Barwell et al., 2021; Bebber et al., 2019; Scott et al., 2019) and of occupied range (e.g., Feldmeier et al., 2016; Kriticos et al., 2013; Yonow et al., 2013). For crop pests including herbivorous arthropods, pathogenic microbes, and virus species numbers within regions are predicted to be higher than observed levels (Bebber et al., 2019) and hotspots of pest invasion are located in Mesoamerica, Europe, North-East Asia and Australia (Bebber, 2015).

Global plant pathogen studies project an increase in potentially suitable areas, especially towards higher latitudes (Avila et al., 2019; Burgess et al., 2017). While for some pathogens (e.g., *Phytophthora cinnamomi* (Phytophthora dieback); Burgess et al., 2017) the entire potential future environmental range is modelled, other approaches couple both the pathogens and hosts when modelling future ranges (e.g., *Diuraphis noxia* (Russian wheat aphid), Avila et al., 2019). Additionally, there are approaches that extend distributional invasion risk measures by impact assessments that assess the overlap of the potential future distribution and cropland area (e.g., *Raoiella indica* (red palm mite); Amaro & de Morais, 2013). Pathogen distribution in many cases is linked to introduced invasive alien species that act as host species and projected invasions thus are inferred from host species presence and distribution change (e.g., chytridiomycosis; O'Hanlon et al., 2018). Crop pests are projected to shift poleward under climate change and increased human activities (Bebber et al., 2013; Fisher et al., 2012, 2020) and under current observed trends the main crop producing countries will be saturated with crop pathogens by 2050 (Bebber et al., 2014). In the marine realm, projections of planktonic and benthic species, as well as algae, identify a future potential poleward shift of alien species under climate change scenarios (Goldsmit et al., 2020; Seebens et al., 2016).

2.6.5. Limitations for assessing future dynamics

Projections of future dynamics of alien and invasive alien species are severely limited by 1) data availability of past and current distributions of species, 2) knowledge gaps of the past and current distribution of species, 3) knowledge gaps of the understanding of causal relationships between species occurrences, environmental changes, drivers of change in nature, biological invasions, and impacts caused by invasive alien species, 4) lack of models to robustly predict future dynamics of biological invasions, and 5) the lack of scenarios covering a range of plausible future dynamics of drivers of change, which would allow exploring future trends under different scenarios. While models and scenarios can still be further developed, closing data gaps, particularly of historic distributions, is very difficult and even impossible in many cases.

Most global studies focus on either individual species or different subsets of species based on specific characteristics (e.g., the 100 of the worst global invaders as assessed by the IUCN ISSG; Bellard, Thuiller, et al., 2013; Gallardo et al., 2017) or on technical criteria such as data availability. Consequently, it is difficult to discern a comprehensive pattern of potential future alien species richness and distribution for individual taxonomic groups (but see Seebens, Bacher, et al., 2021). Additionally, information on alien species distributions is not spatially and taxonomically homogeneous and is biased towards specific regions of the world, like Europe and Northern America (A. C. Hughes et al., 2021; C. Meyer et al., 2016). Although online portals for storing biodiversity data such as GBIF provide billions of occurrence records, the data still covers just a fraction of known species. This limitation in accessibility to species occurrence data severely hampers modelling approaches for predicting and projecting future alien species richness and distribution patterns (**Chapter 1**, **section 1.6.7.3**).

A major challenge for most groups of microorganisms and fungi is the delineation of their native range resulting from a lack of data for these groups in general, as well as from high taxonomic uncertainty due to frequent historic changes and adaptations of the taxonomic concepts (e.g., due to new technological advancements; De Clerck et al., 2013; Essl et al., 2018; Hao et al., 2020; Sharma et al., 2015). In the absence of the ability to distinguish between the native and alien range of a species, robust risk assessments and predictions on the potential future spread and distribution are not possible.

In addition, alien pathogen research largely focusses on human pathogens, livestock, and cultivated plants, neglecting other facets of biodiversity and ecosystem services (Fischer et al., 2012; Peeler et al., 2011; Roy et al., 2017; Usher, 1986). Further, most invasive alien pathogens are only described

once their impacts are recognized in the invaded range (Roy et al., 2017) hampering the identification of potential future alien species risk assessments. Finally, many pathogens undergo host shifts in the invaded range (McTaggart et al., 2016; Peeler et al., 2011; Roy et al., 2017), which can strongly affect disease-induced host mortality in the invaded range, which increases with the evolutionary distance between the native and alien host species (Farrell & Davies, 2019). Such information of host-pathogen associations and interaction however are skewed to few well-studied alien pathogens (Farrell & Davies, 2019).

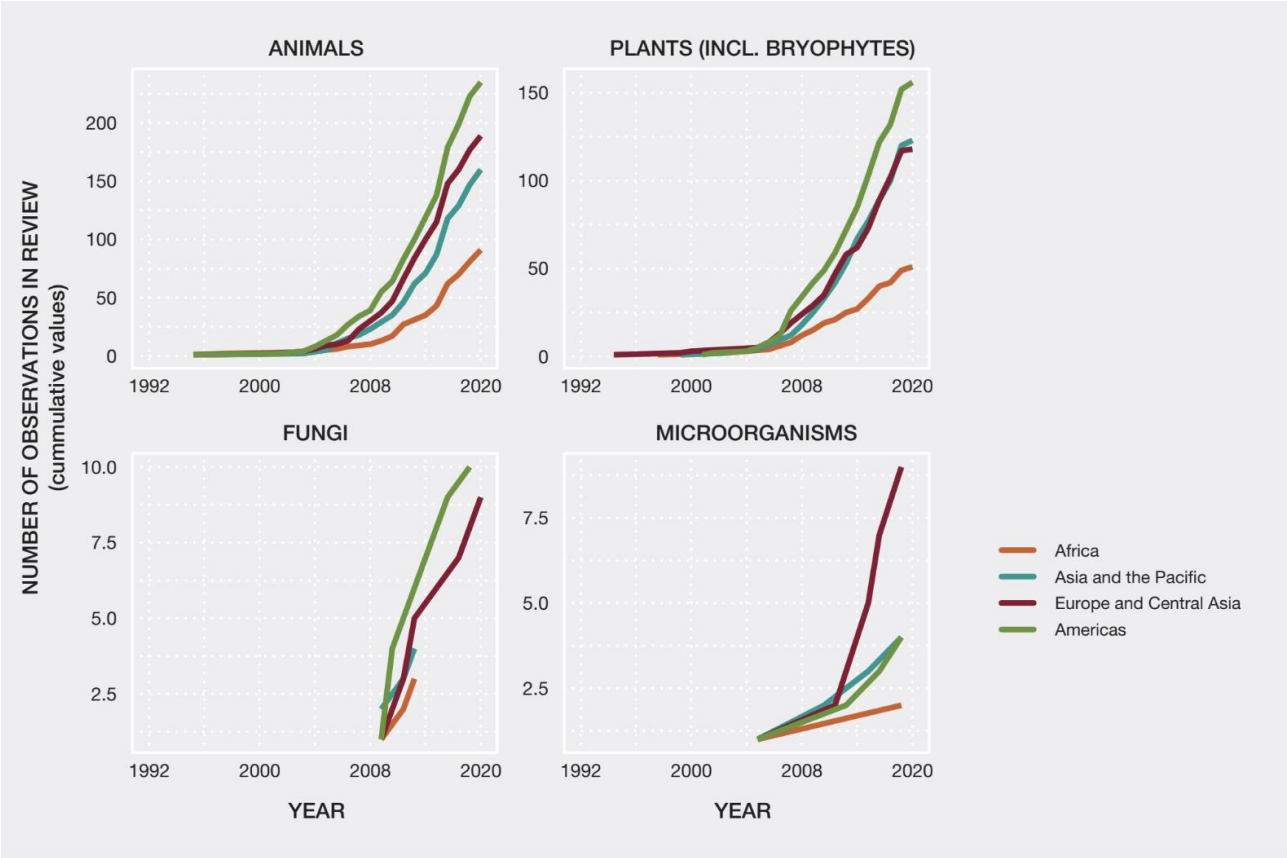

Figure 2.39. Trends in the number of analyses of future projections across IPBES regions. Number of observations is not equal to the number of studies as studies can report on more than one IPBES region and/or taxonomic group. The time reported on the y-axis refers to the date of publication of the respective study. Values are based on a comprehensive literature review about scenarios and models of biological invasions, a data management report is available at https://doi.org/10.5281/zenodo.5706520

The systematic literature review of the models and scenarios[9] revealed distinct trends and research gaps. Research is mainly focused on the Americas, followed by Europe and Central Asia, and Asia and the Pacific, indicating a large knowledge gap in models and scenario studies for Africa. The number of studies is accelerating at an equal pace across IPBES regions (**Figure 2.39**). Plants and animal studies are the most studied taxonomic groups; however, when further separating animals into finer classes, it is clear that animal studies are dominated by research on invertebrates and overall plants are the predominantly studied group, which is consistent over time. Studies for fungi and microorganisms are lacking (**Chapter 1, section 1.6.7.3**). Studies projecting alien species distributions into the future are largely lacking for the marine realm and also not very numerous for freshwater regions compared to the terrestrial realm. While the number of studies has accelerated over time, it is more prominent in the terrestrial realm and especially in the Americas (**Figure 2.40**).

[9] Data management report available at: https://doi.org/10.5281/zenodo.5706520

Finally, most scenario projections explore long-term (2050-2100) and short-term (until 2030) trends. Very few studies follow a backcasting approach that involves setting a desirable future end-point and determining possible pathways including policy measures to reach that end-point (Dreborg, 1996).

To summarize, there is a distinct lack of model and scenario studies for Africa and Asia and the Pacific, the marine and freshwater realms. Finally, the scientific literature is dominated by correlative models whose application has increased more rapidly than for other modelling approaches. Also, process-based models have accelerated in their application; however, the application of hybrid models that combine both correlative and process-based approaches is not very common. Expert-based systems are not utilized for model and scenario studies implying a major gap in the utilization of these knowledge systems. A comprehensive overview of the review can be found in **Chapter 1**, **section 1.6.7.3** and on identified gaps in **Chapter 6**, **table 6.10** and **section 6.6.1.1** and all information and data are available in the data management report. [10]

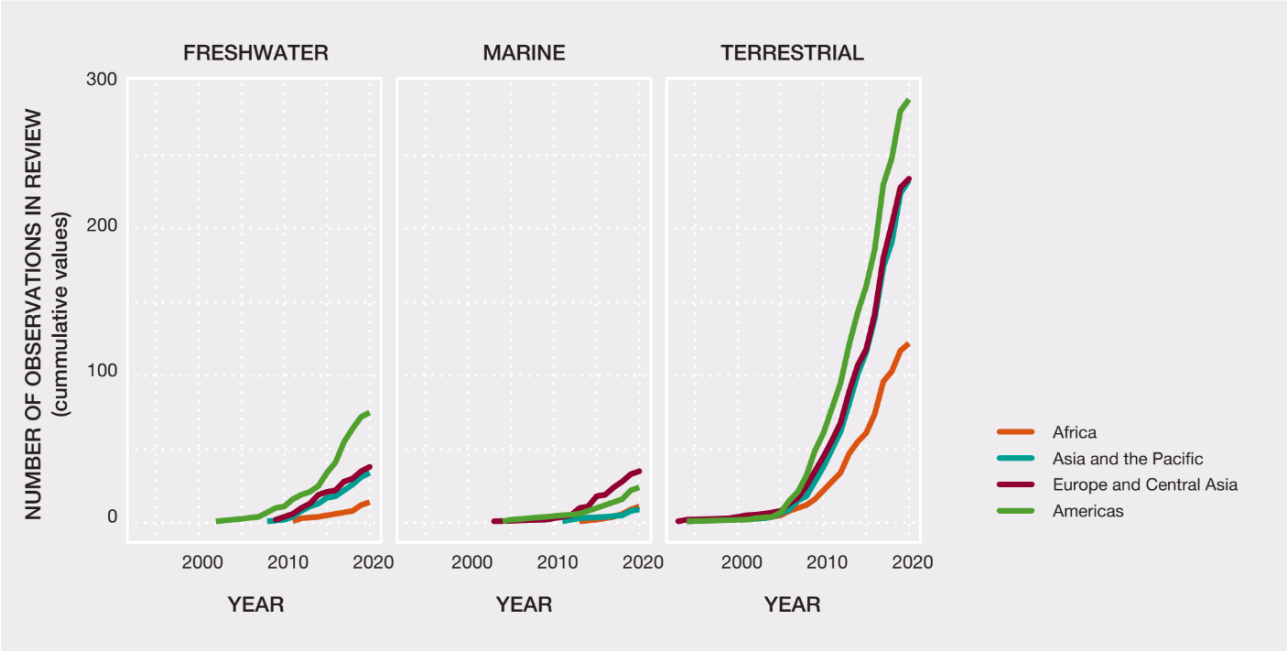

Figure 2.40. Trends in the number of analyses of future projections for realms. Realms are defined as freshwater, marine and terrestrial. Number of observations is not equal to the number of studies as studies can report on more than one IPBES region and realm. The time reported on the y-axis refers to the date of publication of the respective study. Values are based on a comprehensive literature review about scenarios and models of biological invasions, a data management report is available at https://doi.org/10.5281/zenodo.5706520

Finally, in addition to data and knowledge gaps, the prediction of future dynamics of biological invasions is severely impeded by a lack of models to predict those dynamics and by scenarios to explore variations among plausible futures. Although several modelling approaches exist for individual species, regions, or drivers as presented above, no models are available to simulate biological invasions at large spatial and temporal scales, including a range of different species, drivers and impacts. In addition, quantitative scenarios of biological invasions are missing, which hampers the prediction of biological invasions under different plausible futures of driver developments. Qualitative scenario description recently became available (Roura-Pascual et al., 2021), but the quantification and applications in modelling exercises remain to be tested. The field of biological invasions is distinctly lagging behind the progress of other drivers of change in nature,

[10] Data management report available at: https://doi.org/10.5281/zenodo.5706520

such as climate change and land-use changes, where much more attention has been paid over recent decades to develop models and scenarios.

2.7. Conclusions

The main objective of this chapter was to provide a global overview of the current understanding of the temporal trends and the spatial distribution (i.e., status) of alien and invasive alien species. By conducting extensive literature reviews and consulting experts from all over the world, assessment experts have gathered information on the trends and status of alien and invasive alien species across a wide range of taxonomic groups, geographic regions, and ecosystems. This assessment strove to provide an overview, which is as balanced as possible in terms of geographic and taxonomic coverage of species. However, complete coverage across all taxa, habitats, and regions is not possible due to many data and knowledge gaps. In some cases, the widespread gaps make a truly global and extensive assessment of the trends and status difficult. In addition, even well-sampled taxa and regions likely have incomplete information. Although this assessment considered a huge number of publications, including scientific publications, reports, and books in various languages, and consulted many experts, many sources of information could not be considered in this chapter, particularly non-English publications and grey literature, which are difficult to access if experts from that field or region are not directly involved.

Although this chapter provides the most comprehensive assessment of the trends and status of the distribution of known alien and invasive alien species, it is nonetheless based on incomplete data, the extent of which varies by taxa, region, and habitat. However, the existence of such gaps does not imply that any robust conclusions cannot be drawn. In fact, there is a good understanding of the trends and status of alien species for many taxonomic groups and regions, which are presented in this chapter, and the most robust and general conclusions are shown in the executive summary at the beginning of this chapter. However, with incomplete data it is necessary to verify available information by assessing trends and status based on scientific expertise and taking underlying biases into account.

Biological invasions are complex and intertwined with human transportation and goods, as well as other components of global change such as land use change, climate change, and human disturbances. This ecological complexity, the diversity and abundance of alien species, and the difficulty of identifying invaders in new environments, make their prevention and management challenging. The data presented in this chapter demonstrate that there is almost no place on Earth that has not experienced alien species introductions. It also shows that alien species introductions to new ranges are increasing across all taxa, all IPBES regions, and all units of analysis and that there are large data and knowledge gaps across these three sectors. The immediate result is that biological invasions are underestimated, with many species not yet identified as invasive and many ecosystems not yet recorded as invaded, or invaded by all the alien species that are present.

Decision makers often interpret research and develop policies to address biological invasions based on incomplete and biased data. Identifying and closing these data and knowledge gaps is essential to assess and address biological invasions more accurately and comprehensively. While gathering the information underlying this chapter, experts have identified the following major limitations which hindered the assessment:

1. **Lack of regional alien species lists**: For many taxonomic groups, particularly among invertebrates and microorganisms, lists of reported alien species are lacking for many countries. Even for ecologically and economically important groups such as insects, such lists are often lacking.
2. **Incomplete data**: Available lists of alien species occurrences are often incomplete or outdated. While difficult to identify, a comparison of alien species numbers across countries often revealed strong differences among neighbouring countries, differences that are likely influenced by degree of survey intensity rather than actual occurrences. In addition, the spread of alien species is highly dynamic and thus maintaining an up-to-date list of alien

species occurrences requires regular monitoring which is rare. Even more rare are data on the abundances of individual populations. They are so scarce that experts were unable to consider alien species population abundances in this chapter.

3. **Lack of standardization**: Available lists of alien species were often generated using different terms that vary in their definitions, concepts (including taxonomies), and data collection and sampling practices, making comparisons of available information across regions and taxa difficult. This is particularly problematic for distinguishing a species' invasion status such as introduced, established, and invasive; these distinctions are often not specified, and if they are, the applied definitions are often not provided. Ideally, data is reported using standard concepts and terminologies, which are also explicitly detailed in the description of the data.
4. **Coarse spatial resolution**: The information on alien species occurrences is usually provided only at a coarse spatial resolution, such as the country level. However, the distribution of alien species within a country is often aggregated towards certain geographic areas within national borders. For a thorough assessment of biological invasions across spatial scales, it is essential to obtain information at finer resolutions that are ideally associated with coordinates of alien species occurrences.

Closing these gaps poses huge challenges to the scientific community. Below is a list of a few key challenges to improving assessments of the trends and status of alien and invasive alien species.

Improving collaboration

To fill data gaps and make invasion science truly global, greater, and more equitable, international collaboration is needed to build more global networks for monitoring, data sharing, and technology transfer (Kuebbing et al., 2022; Meyerson et al., 2022; Nuñez et al., 2021; Packer et al., 2017). The trend towards open-source software, such as QGIS and statistical environments such as R, is helping to reduce disparities between rich and poorer regions, but costs associated with training scientists and executing research as well as prohibitive journal publication costs present serious obstacles (**Chapter 6**, **section 6.6.2.4**). Many invasive alien species-focused research networks, database repositories, intergovernmental and international organizations, and international agreements are already in place (reviewed in Meyerson et al., 2022). Despite these efforts, additional coordination and collaboration are needed, particularly because individual countries often do not have the capacities to respond to the issues of biological invasions sufficiently (**Chapter 6**, **section 6.3.1.1**; Early et al., 2016; Pyšek, Hulme, et al., 2020). In addition, it would be beneficial to engage in a two- or multi-way discussion with public and stakeholders through a new "dialogue communication model" or "public engagement model" (**Chapter 5**, **section 5.2.1**; **Chapter 6**, **section 6.4**), based on a genuine interchange with the public that recognizes and incorporates differences in knowledge, values, perspectives, and interests (Courchamp et al., 2017). This will allow better understanding of biological invasions and supporting data acquisition, research and management.

Closing knowledge gaps

Thoroughly assessing the trends and status of biodiversity requires deep knowledge about nature and the ecosystems supporting biodiversity. Without knowing the species and their life histories, their interactions, and the mechanisms shaping environments worldwide, the state of biodiversity cannot be fully assessed. While information about nature is accumulating at an unprecedented pace, there are still major knowledge gaps, particularly for relatively inconspicuous organisms such as invertebrates, fungi, and microorganisms, and less accessible systems such as in marine habitats, but also inland waters, and in geographic areas such as Central Africa, Central Asia, and remote islands. In addition, there is a lack of an adequate understanding of biotic and abiotic species interactions, without which experts cannot fully grasp how species respond to environmental

changes nor build models predicting future biodiversity change under different scenarios of human development. Closing these knowledge gaps is therefore essential to fully inform policies that can safeguard nature and move societies towards sustainability.

Efficient and standardized sampling and data processing

Comprehensive and thorough assessments of biological invasions and biodiversity in general need global and comprehensive monitoring and databases (Latombe et al., 2017; Meyerson et al., 2022; Packer et al., 2017), which can only be obtained by implementing the following:

- Collection of records of alien species occurrences, and regular and repeated deposition into publicly accessible databases, particularly in regions and for taxonomic groups with the most severe gaps.
- Mobilization of existing data by making it accessible to the wider community in electronic formats and by providing these data under the Findable, Accessible, Interoperable, Reusable (FAIR) principles of open science (Wilkinson et al., 2016).
- Standardization of available and accessible data to allow comparison, which could be accomplished by adopting a standard terminology for biodiversity information as Darwin Core has done, and by using open and widely used data formats such as csv or txt (Groom et al., 2019).
- Documentation of data transformation steps, ensuring that they are repeatable and associated with the data (Seebens et al., 2020).
- Finally, integration of standardized data into open databases or data portals such as GBIF or the Ocean Biodiversity Information System (OBIS) to enable researchers and stakeholders to conduct tailored biodiversity assessments.

Ideally, all steps from recording to storing data would follow standard and published protocols to make science, decision-making, and the assessment of biodiversity comprehensive, transparent, interoperable and reproducible, which ultimately increases trust in results and decisions (e.g., De Pooter et al., 2017; Groom et al., 2017; Haider et al., 2022; Roy et al., 2018).

Technological advances

Similar to the increase in information, technologies are developing rapidly including those designed to monitor biodiversity. Advances range from new satellite products to environmental DNA to fully automated biodiversity measurement stations. For example, satellites now provide opportunities to measure not only vegetation patterns at high resolution but also to track the movement of species or to distinguish individual plant species and measure plant traits which can provide early detection of new alien species introductions. Likewise, environmental DNA can help to populate lists of species occurring in certain areas, including rare species and emerging new alien species. Cameras and pattern recognition through artificial intelligence can identify species at comparatively low cost but on large geographic scales. Drones can now monitor biodiversity and fully automated biodiversity stations similar to weather stations are currently developed to obtain high resolution recordings of biodiversity. However, although these developments are promising, the technologies often still require major advancements to get ready for measuring biodiversity at the species level. In addition, many technological solutions are still used in isolation and large-scale solutions to obtain comprehensive coverage of biodiversity monitoring have not yet been achieved.

Engagement with policy makers

Progress towards addressing data gaps for biological invasions can benefit from engagement by policy makers, funding, trained (citizen) scientists, and technicians, adequate infrastructure to achieve standardized tools for long-term monitoring, modular regulatory frameworks that integrate incentives and compliance mechanisms with respect for diverse transcultural needs, biosecurity

awareness and measures and synergies with other conservation strategies (Meyerson et al., 2022; **Chapter 5**, **section 5.4.3.2(a)**; **Chapter 6**, **section 6.6.2.1**).

Inclusive biodiversity monitoring (citizen science, Indigenous Peoples and local communities)

Global comprehensive taxonomic monitoring of alien and native biota could be improved through engagement with people outside of academia, agencies, and institutions. People interested in nature and willing to contribute to recording of species occurrences could be encouraged to provide their knowledge and findings to other people and databases through, for example, community science projects, participatory research programmes and online platforms such as iNaturalist, CoralWatch, Project Noah, or e-Bird (Aristeidou et al., 2021; Ballard, Dixon, et al., 2017; Ballard, Robinson, et al., 2017; McKinley et al., 2017; **Chapter 1**, **Box 1.15**; **Chapter 6**, **section 6.6.2.1**). Such a large scale, ideally global, data reporting and sharing programme requires, however, concerted efforts of the international community and thus would benefit from greater efforts and incentives by governments and institutions to encourage people to contribute. Obtaining data through community science of sufficient quality for use in biodiversity assessments can be achieved through concerted coordination and organization, training, guidance, and funding. Standards for sampling and reporting have to be defined and adhered to, and needs and goals must consider the requirements of individual communities. In this way, inclusive biodiversity monitoring would include Indigenous Peoples and local communities who have a deep understanding about those areas that are least represented in global biodiversity assessments. Such an approach to fill data gaps for alien and invasive alien species is inclusive, adaptive, and flexible. As integrated and collaborative networks develop, effective global strategies to address invasive alien species will finally be met.

Accounting for incomplete knowledge

Several data gaps could be filled by increasing efforts and investments into biodiversity research and monitoring. However, it seems unlikely that obtaining complete and regular data at large geographic scales is achievable. Thus, it is also necessary to not only acknowledge the lack of information, but to also quantify uncertainty and incompleteness of data and to explicitly account for those biases in biodiversity assessments and analyses. This requires the development and adoption of standardized methods to quantify uncertainty. Having a standardized approach to measure and account for incomplete data would increase robustness of the results, and increase confidence in individual reports of biological invasions and biodiversity research more generally (Franz & Sterner, 2018).

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